Mesocarnivores in Protected Areas: ecological and anthropogenic determinants of habitat use in northern Kwa-Zulu Natal, South Africa.

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By

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PANTHERA

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ABSTRACT

Protected areas (PAs) form the cornerstone for most carnivore conservation strategies. However, climate change, increased isolation and human pressure along PA boundaries are together reducing the effectiveness of PAs to conserve carnivores. Mesocarnivores, in particular, frequently move beyond the boundaries of PAs where they threaten human livelihoods, and as a result, are often subject to chronic persecution. In South Africa, we know little about the conservation status of mesocarnivores both within and outside of PAs, as most research focuses on large, charismatic apex predators. The goal of my study was to leverage data collected from large carnivore studies to understand variation in mesocarnivore species richness within PAs. Camera trap surveys were conducted as part of Panthera's 2015 national leopard monitoring programme in seven PAs across northern KwaZulu-Natal (KZN), South Africa. Using a multi-species extension of the Royle-Nichols occupancy model, my study explored environmental, interspecific and anthropogenic drivers of mesocarnivore habitat use and species richness. I found a surprisingly low number of detections (N = 356) for all five mesocarnivore species and considerable variation across PAs. Small PAs with a recent history of human disturbance supported more mesocarnivore species and at higher relative abundance. Mesocarnivore species richness was found to decline with increased vegetation and leopard abundance but increased towards the edge of PAs. Variation in species richness estimates decreased significantly with vegetation productivity and domestic dog abundance. Together these results suggest that (1) the edges may provide a refuge for mesocarnivores from more dominant species, (2) mesocarnivores exhibited resilience/adaptability to human disturbance, and (3) primary productivity and domestic dog abundance could mediate mesocarnivore distributions within PAs. My study showed that camera trap data derived from a single-species survey can be used to make inferences about non-target species to great success. Current PAs in KZN may not adequately conserve mesocarnivores, and as a result, emphasis should be placed on coexistence with mesocarnivores in marginal habitat outside of PAs.

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1 | LITERATURE REVIEW

1.1 | Carnivore conservation

Protected areas (PAs) cover 14.7% of the world's terrestrial surface (IUCN and UNEP-WCMC, 2019) and are the cornerstone of most carnivore conservation strategies (Hansen and DeFries, 2007; Caro *et al.*, 2014). They also form a central component of sub-Saharan Africa's tourism industry, valued at US$25 billion and provide 2.4% of employment in the region (World Travel and Tourism Council, 2017). Whilst PAs have been acknowledged as important for conserving biodiversity (Brooks *et al.*, 2006), they are facing a wide variety of threats across a range of spatial scales which together are reducing their conservation potential, especially for carnivores (Balme, Slotow and Hunter, 2010; Radeloff *et al.*, 2010; Watson *et al.*, 2014; Santini *et al.*, 2016). These threats include climate change (Tanner-McAllister, Rhodes and Hockings, 2017), increased isolation (DeFries *et al.*, 2005), invasive species (De Poorter, 2007) and an increase in anthropogenic impacts close to PA boundaries (Zommers and Macdonald, 2012), such as human-livestock-wildlife conflict (Bruner *et al.*, 2001), and the exploitation of natural resources (Goodman, 2006; Smith *et al.*, 2009; Becker *et al.*, 2013; Caro *et al.*, 2014). These impacts and their adverse effects on biodiversity are predicted to be disproportionately greater in developing regions, such as sub-Saharan Africa, largely due to predicted increases in human populations and the associated developmental changes (Pettorelli *et al.*, 2010).

Carnivores, in particular, have experienced substantial population declines in recent years (Di Minin *et al.*, 2016). In 2014, meta-analyses on global carnivore conservation revealed 77% of extant terrestrial carnivore species are undergoing continuing population declines, with 24 of these species under direct threat from human persecution (Ripple *et al.*, 2014). For example, the Ethiopian wolf (*Canis simensis*) has experienced dramatic population declines since 2008 chiefly due to habitat degradation through subsistence farming and consecutive epizootics of rabies and canine distemper (Marino and Sillero-Zubiri, 2011; Gordon *et al.*, 2015). Characterised by wide-ranging behaviour, carnivores frequently move beyond the boundaries of PAs where they pose a threat to human lives, as well as livelihoods, and are often subject to persecution (Treves and Karanth, 2003). Even within the confines of PAs, direct poaching

can lead to "edge effects"[1]. This may result in total population declines of carnivores and their prey if balance is not achieved through recruitment (Balme, Slotow and Hunter, 2010; Johnson *et al.*, 2016; Rosenblatt *et al.*, 2016; Carter *et al.*, 2017; Rogan *et al.*, 2018; van Eeden *et al.*, 2018).

Increased anthropogenic pressure could favour species with greater adaptive plasticity (Anderson, Panetta and Mitchell-Olds, 2012; Wang *et al.*, 2017). Dietary breadth[2] and behavioural adaptability allow species to better mediate against environmental changes and threats (Wong and Candolin, 2015). Large carnivores are often prey specialists and invariably fulfil the role of apex or keystone species within ecosystems (Ripple *et al.*, 2014), making them more susceptible to anthropogenic disturbance. By contrast, mesocarnivores[3] are typically generalist predators, and as such exhibit weaker ecological interactions within the ecosystems that they live (Roemer, Gompper and Van Valkenburgh, 2009). This makes mesocarnivores less vulnerable to extinction compared to larger carnivores (Purvis *et al.*, 2000). However, there has been evidence to suggest that mesocarnivores can provide vital ecosystem services through seed dispersal (Kurek and Holeksa, 2015; Twigg, Lowe and Martin, 2016), small mammal control (Ramnanan *et al.*, 2016) and the removal of dead animals, especially in systems lacking obligate scavengers, such as vultures (Mateo-Tomás *et al.*, 2015). Thus, reductions in mesocarnivores could be detrimental to overall ecosystem functioning and human health (Ćirović, Penezić and Krofel, 2016).

The majority of studies (86%) exploring the relationship between apex predators and mesocarnivores show a strong inverse relationship (Ritchie and Johnson, 2009). Apex predators suppress mesocarnivore abundance through direct competition and predation (Wang, Allen and Wilmers, 2015). Declines in apex predator abundance have often been shown to result in population expansions of mesocarnivore species, known as mesocarnivore

[1] Changes in population or community structures occurring at habitat borders (Levin, 2009).
[2] Dietary breadth is the range of food items a species can consume that will maximize the cost/benefit function of energy per unit of foraging time (Hames and Vickers, 1982). Having a greater diversity in foraging choice can help buffer against changes in prey perturbations.
[3] Carnivore species, also referred to as mesopredators, weighing between 1-15kg (Buskirk, 1999) that hold an intermediate trophic level (Prugh *et al.*, 2009).

release[4]. This release mechanism has been linked to a negative association between body size and species richness (Gittleman and Purvis, 1998). This is based on the theory of allometric ecology, whereby average adult body size (i.e., weight) is strongly related to both physical and behavioural traits (Damuth, 1981). An animal's body size ultimately determines its relative energy requirements, influencing both its prey selection and hunting strategies (Carbone and Gittleman, 2002; Radloff and Du Toit, 2004; Owen-Smith and Mills, 2008). However, the theory of mesocarnivore release is still debated with Allen *et al.* (2013) and Hayward and Marlow (2014) strongly criticising the methods surrounding the theory, covering a wide variety of methodological flaws, sampling bias and experimental design constraints. This is particularly relevant for management practices using apex predators to directly suppress mesocarnivores, such as using dingoes (*Canis lupus dingo*) to manage introduced red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) in Australia, as the assumption of top-down control may not always hold.

An animal's weight has also been linked to a variety of critical ecological variables such as population density (Johnson, 1999), home range size (Ofstad *et al.*, 2016), dispersal capabilities (Forero-Medina *et al.*, 2009; Bailey *et al.*, 2018), foraging efficiency (Rizzuto, Carbone and Pawar, 2018) and fecundity (Allainé *et al.*, 1987). Mesocarnivores, being smaller than apex predators, typically outnumber them by as much as 9:1 (Carbone and Gittleman, 2002; Roemer, Gompper and Van Valkenburgh, 2009). This ratio becomes more skewed as mesocarnivores expand to fill vacant niches left by the local disappearance of larger predators.

The ability of mesocarnivores to rapidly increase in number and exploit both small livestock on farms and waste within peri-urban areas (Berger, 2006; Prugh *et al.*, 2009; DeVault *et al.*, 2011; Ripple *et al.*, 2014) has meant they are often assigned the status of pest. For example, within South Africa, black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*) have dramatically increased in range and abundance following the extirpation of large carnivores throughout commercial farming areas (Thorn *et al.*, 2012; Drouilly and O'Riain, 2019). While it is not known what impact apex predators would have had on livestock it is now well

[4] An ecological hypothesis whereby decreases in apex predators lead to substantial growth in mesocarnivore populations (Prugh *et al.*, 2009).

established that mesopredators on farmland are causing significant depredation of sheep (*Ovis aries*) and goat (*Capra hircus*), ultimately threatening farmer livelihoods (Drouilly, Nattrass and O'Riain, 2018; Turpie and Babatopie, 2018). Black-backed jackals in particular are a concern within rural landscapes given the increased risk of disease transmission, such as rabies (Butler, Du Toit and Bingham, 2004), and their preference for livestock over wild prey (Drouilly, Nattrass and O'Riain, 2018). In a survey conducted by Badenhorst (2014), six of seven South African provinces ascribed the majority of their cattle (*Bos taurus*) depredation to black-backed jackal. Consequently, black-backed jackals are heavily persecuted on farmland both by individual hunters and organised culling events (Zimmermann *et al.*, 2009; Turpie and Babatopie, 2018).

1.2 | Factors affecting the composition of mesocarnivore communities

Changeable, complex environments favour generalists as they can rely on several resources (Clavel, Julliard and Devictor, 2011). Hence, studying generalists requires the examination of numerous interacting variables. The composition of mesocarnivore communities within PAs are shaped by various, interacting factors such as habitat requirements, interspecific relationships, human pressure and PA attributes (Tambling *et al.*, 2018). For example, swift fox (*Vulpes velox*) density was found to be negatively influenced by coyote (*Canis latrans*) abundance, but this relationship was moderated by basal prey availability and vegetation structure (Thompson and Gese, 2007).

In general, carnivore distributions within PAs have been shown to be greatly affected by the presence of permanent water, with increased mesocarnivore occupancy closer to water sources (Schuette *et al.*, 2013; Rich *et al.*, 2017). Dense vegetation, commonly located around drainage lines, can provide concealment during hunting and refugia from interspecific predation (Boydston *et al.*, 2003). Such areas surrounding water sources also offer increased hunting and scavenging opportunities. For example, black-backed jackals have been observed killing ungulate calves and a variety of small antelope species next to water sources (Krofel, 2007). African wild cat (*Felis silvestris lybica*) and civet (*Civettictis civetta*) also show strong inverse correlations between occupancy and distance to water (Durant *et al.*, 2010). Increased habitat variability and structural complexity, i.e., diverse vegetation and terrain,

will also favour mesocarnivores, as it caters to a more generalist niche (Roemer, Gompper and Van Valkenburgh, 2009; Wilson *et al.*, 2010). For example, caracals have been shown to prefer rugged terrain that provides both safe sleeping sites and increased ambush opportunities when hunting (Drouilly *et al.*, 2018).

Prey abundance is thought to directly influence carnivore density (Karanth *et al.*, 2004). However, the relationship between prey abundance and carnivore presence is complicated and can be influenced by a multitude of factors, such as interspecific predation and competition, as well as prey turn-over rates (Fuller, 1996). Flexibility in mesocarnivore diet enables them to adapt to changes in prey availability (Carbone and Gittleman, 2002), potentially diminishing the impact of prey abundance on total mesocarnivore density. Caracals and black-backed jackals have been shown to be only marginally affected by changes in their prey base (Minnie *et al.*, 2018).

Understanding how local prey populations drive mesocarnivore presence is vital, however, reliable prey abundance estimates are difficult to obtain. Relative Abundance Indices (RAIs) can be calculated from animal signs (e.g., tracks or faecal counts), road-kill accounts or photographs from remote camera traps, whereby the number of detections is used as a proxy for species abundance. However, these results can be considerably error prone due to the assumption that all species have an equal probability of being detected over time and space (Sollmann *et al.*, 2013; Iknayan *et al.*, 2014). For example, carnivores are often assumed to use roads as a mode of travel (Hines *et al.*, 2010; Poessel *et al.*, 2014; Burton *et al.*, 2015) and consequently many studies exploring carnivore occupancy or abundance survey along road networks to increase detection probability. However, there is evidence that prey species are indifferent to roads, or actively avoid them, and therefore, using RAIs derived from a road based survey would lead to inaccurate assessments of prey availability (Harmsen *et al.*, 2010; Mann, O'Riain and Parker, 2015). It is thus difficult for any one method (e.g., camera traps or tracks) or survey design (paths, roads or random) to provide accurate and cost-effective estimates of both predator and prey species abundance.

Interspecific interactions play a major role in determining carnivore population density (Fuller, 1996). Interspecific predation and competition can lead to changes in species

abundances within PAs, as a result of elevated levels of aggression and kleptoparasitism. On average, an African carnivore will experience exploitative competition with 22.4 other species (Caro and Stoner, 2003). Mesocarnivore species are particularly vulnerable to kleptoparasitism with 13 different species stealing food from black-backed jackals, 10 from serval (*Leptailurus serval*), 9 from caracal and 3 from side-striped jackal (*Canis adustus*; Caro and Stoner, 2003). Subordinate carnivores, such as the Altai mountain weasel (*Mustela altaica*), have been shown to spatially and temporally shift their behaviour to avoid its more dominant competitors, stone martens (*Martes foina*) and red foxes (Bischof *et al.*, 2014). Due to the inherent functional diversity present in the mesocarnivore guild, they can exploit a broad prey base (Roemer, Gompper and Van Valkenburgh, 2009; Rich *et al.*, 2017), and as a result, can exhibit a variety of responses to similar external pressures. Caracals, for example, have been observed to be more successful in the absence of apex predators than black-backed jackals (Drouilly *et al.*, 2018). Therefore, the relationship between large and mesocarnivores may reflect a complex balance of risk-avoidance and energy requirements, all of which may be influenced by anthropogenic disturbances.

Human presence on the boundaries of PAs can be detrimental to the overall health of the PA (Hansen and DeFries, 2007; Radeloff *et al.*, 2010). Reduction and/or degradation (from direct habitat loss, or noise and light pollution) in the areas around a PA can greatly reduce its functional size. Subsequently, as core area size is reduced, animals at higher trophic levels, such as large apex predators, are the first to become locally extinct (Ripple *et al.*, 2014) . This can lead to trophic cascades or mesocarnivore release within a PA (Treves and Naughton-Treves, 2005; Yarnell *et al.*, 2013). Human presence can also lead to the destruction of potential corridors between PAs, or ephemeral lands, restricting dispersal and gene flow between protected populations. Finally, increased exposure to humans at the edge of PAs can lead to population sinks, caused by legal offtake through hunting, illegal poaching, the introduction of invasive species and diseases, or increased human-wildlife conflict. Radeloff *et al.* (2010) showed that housing growth within a 1km buffer of PA boundaries exerted a direct influence on the wildlife within.

The introduction of domestic and invasive animals by local communities has a large negative impact on carnivore species (Hughes and Macdonald, 2013; Zapata-Ríos and Branch, 2016).

The proximity of livestock to PA boundaries increases retaliatory killing (Berger, 2006; du Plessis *et al.*, 2015), as livestock provide a plentiful and easy prey resource for carnivores. Domestic dogs (*Canis familiaris*) pose a significant threat to native carnivores by acting as competitors, predators and disease vectors (Young *et al.*, 2011; Silva-Rodríguez and Sieving, 2012; Gompper, 2013; Zapata-Ríos and Branch, 2018). Domestic dogs are found in higher densities in more human-dominated areas (Odell and Knight, 2001; Ordeñana *et al.*, 2010) and where agricultural land borders PAs. The presence of domestic dogs in PAs and their associated threats to native species are most significant at the borders, showing a decreasing trend to the interior of the PA (Torres and Prado, 2011). Therefore, dogs could exacerbate edge effects associated with the peripheries of PAs (Revilla, Palomares and Delibes, 2006).

All of these anthropogenic influences may manifest as edge effects; increased mortality rates close to or beyond the reserve boundaries, causing these peripheral areas to become population sinks (Woodroffe & Ginsberg 1998). Edge-dwelling species are positively affected by changes in the core:edge ratio of a PA. Mesocarnivores might not be effected by edge effects to the same extent as larger carnivores due to their ecological plasticity (Purvis *et al.*, 2000). However, mesocarnivore responses have been shown to vary depending on species sensitivity to fragmentation and anthropogenic factors (Baker and Leberg, 2018). As mesocarnivores constitute a large portion of road kill and are heavily persecuted due to livestock predation or perceived rabies threats (Noss, 1998), utilising available edge space may be harmful to mesocarnivore abundance due to an increased chance of hostile contact with humans (Crooks, 2002).

1.3 | Camera traps and occupancy modelling as research tools

To improve large scale predator management, it is vital that we understand how carnivore species of all sizes and trophic levels interact with their environment. This requires long-term monitoring of populations, at varying spatial and temporal scales, across a range of climatic and land use gradients.

1.3.1 | Camera trapping theory

Camera trapping has emerged as a popular, non-invasive and cost effective method for monitoring wildlife presence, abundance, activity patterns and density (O'Connor *et al.*, 2017). It allows for longer monitoring periods and larger-scale research than traditional surveying techniques (e.g., scat surveys, line transects or GPS collars), creating the opportunity to study rare, elusive species (Caravaggi *et al.*, 2017).

The advantages of camera trapping are not limited to field work but expand into the data extraction process. Using camera trapping as a means of data collection allows for post-study data verification and analyses by independent observers (Newey *et al.*, 2015; Caravaggi *et al.*, 2017). This enables datasets to be inherited and subsequently re-evaluated under new methodologies or used to explore alternative hypotheses. Additionally, processing time and cost can be greatly reduced by using citizen scientists (non-professional volunteers) for species identification (Kosmala *et al.*, 2016). Artificial intelligence (AI) is also being used to assist in wildlife monitoring (Kwok, 2019). Together these advances have facilitated larger and longer running camera trap surveys as data processing is no longer restricted by researchers' available time or funds. AI can facilitate the quick accumulation and analyses of large datasets ultimately allowing for more robust and timeous conclusions.

The most common use of camera trap data is estimating abundance or density of individually-identifiable species (e.g., tigers (O'Brien, Kinnaird and Wibisono, 2003; Wang and Macdonald, 2009) or leopards (Balme, Slotow and Hunter, 2010)) through spatial capture-recapture modelling. Yet the versatility of camera trapping has allowed for a wide range of applications such as: biodiversity assessments (Ahumada *et al.*, 2011), species discoveries (Rovero *et al.*, 2008) and behavioural studies. Behaviours that have been monitored with camera traps include anti-predator responses (Carthey and Banks, 2015), denning (Miller *et al.*, 2017), foraging (Delgado-V *et al.*, 2011), resource portioning (Edwards, Gange and Wiesel, 2015), social behaviour (Leuchtenberger *et al.*, 2014) and temporal avoidance (Romero-Muñoz *et al.*, 2010). Finally, incorporating presence-absence data from camera traps into occupancy modelling frameworks has facilitated investigations into the drivers of unmarked species

(species with unidentifiable characteristics) distributions and species richness (Kolowski and Forrester, 2017).

1.3.2 | Basic camera trap survey designs

Camera trap survey design (i.e., camera locations, numbers, spacing and length of deployment) should be linked to the overall study objectives (Burton *et al.*, 2015). Studies may prioritise landscape sampling over detection rates, and therefore, design the camera survey so as to accurately sample the available landscape (Kolowski and Forrester, 2017; O'Connor *et al.*, 2017). Spacing within a survey is determined by placing a grid over the study area and apportioning camera stations within each grid (Figure 1.1). Camera traps can be spaced at random in a landscape using a simple random design (e.g., allocating camera locations at random coordinates within a grid) or a systematic random design (e.g., locations are arranged in a regular pattern at equidistance from each other). A clustered camera design can also be used when accessibility within a study area is limited (Figure 1.1). Grid cell size can be determined based on the number of cameras available or on individual home range size of the target species. Some camera trap surveys also bait or use scent lures to increase detection probability (du Preez, Loveridge and Macdonald, 2014).

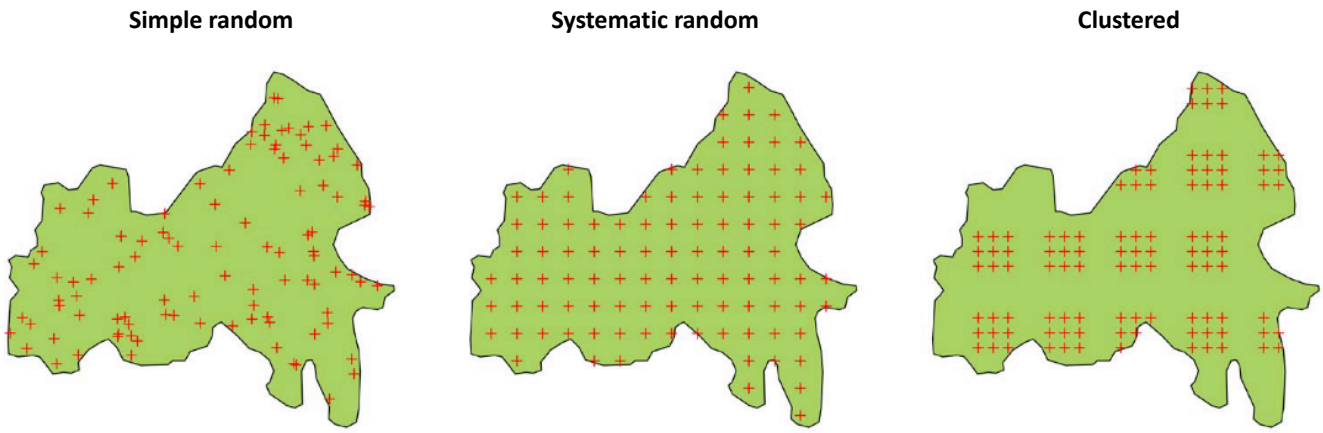

Figure 1.1 Basic sampling designs for camera trap surveys taken from Wearn and Glover-Kapfer (2017)

A large percentage of camera trap surveys (54.8%) use capture-recapture methods based on a targeted probabilistic design (Burton *et al.*, 2015). This is where cameras within each grid cell are purposefully placed along a corridor of animal movement, such as rivers, roads or

trails, so as to maximise the probability of detecting the target species (Karanth *et al.*, 2004; Shannon, Lewis and Gerber, 2014). This limits the usefulness of the data for other purposes, such as in biodiversity estimations or for monitoring non-target species using RAIs (Wearn and Glover-Kapfer, 2017). Also, using such "optimal" camera locations can potentially cause a bias in detection rates, especially when multiple species are being studied (O'Brien, 2011; Swann, Kawanishi and Palmer, 2011; Wearn *et al.*, 2017). However, robust statistical methods, such as occupancy modelling, can mitigate detection biases created by unsuitable camera trapping designs (MacKenzie *et al.*, 2006; Gould *et al.*, 2019).

The success of a camera trapping survey is heavily dependent on individual camera reliability. Camera failure does occur, such as when batteries malfunction, or difficult climatic conditions lead to increased non-animal trigger events which can rapidly saturate a camera's memory or lead to premature battery failure (Swann, Kawanishi and Palmer, 2011). Fortunately, many of these technical failures can be accounted for either in the survey design, i.e., having multiple checks throughout the survey to reduce prolonged camera faults, or during *post hoc* data cleaning, such as correcting erroneous date/time stamps (Shannon, Lewis and Gerber, 2014). Another challenge associated with camera trapping is inconsistency in terminology and underreporting of survey methodology in research papers, preventing reproducibility (Meek *et al.*, 2014).

Sampling error is a common problem with any wildlife surveying method, particularly with regards to imperfect detection. Although a species is present in the sample unit, an individual may not be detected by the camera (MacKenzie *et al.*, 2006). Imperfect detection can occur on multiple levels. Firstly, the animal can use the area within the detection zone but not trigger a capture event, due to its body size, movement speed or wariness for foreign objects (Caravaggi *et al.*, 2017). Secondly, the animal can use the wider area around the camera but not enter the detection zone, i.e., camera traps can only detect movement within a certain radius of the camera's sensor (Burton *et al.*, 2015). Finally, an animal may also become temporally unavailable for detection due to its episodic or mobile nature, or other individuals may immigrate into the study area or be recruited through birth. These challenges can be addressed through repeated surveys and/or by incorporating camera placement features, and other detection variables, into further modelling exercises to reduce the probability of

false absences and prevent misleading conclusions on species distribution (MacKenzie *et al.*, 2006; Royle and Dorazio, 2008; Mordecai *et al.*, 2011).

1.3.3 | Occupancy modelling

Camera trap data is particularly useful for estimating occupancy. Occupancy modelling offers great flexibility, answering a variety of complex ecological questions with relatively simple sampling designs, whilst accounting for imperfect detection. It has been used successfully to explore a variety of different concepts, such as geographic range (Bled, Nichols and Altwegg, 2013), ecological niche partitioning (Schuette *et al.*, 2013), anthropogenic effects on populations and communities (Hames *et al.*, 2002) and resource use (Manly *et al.*, 2002). The flexibility and ease of occupancy modelling has also facilitated multi-species studies which can explore species interactions (Steinmetz, Seuaturien and Chutipong, 2013; Rota *et al.*, 2016; Drouilly, Clark and O'Riain, 2018) and community dynamics (Burton *et al.*, 2012).

The basis of occupancy modelling is to explore what factors determine the proportion of sites occupied by a species. If one assumes that species occupancy (ψ) is independent of any variables, the naïve estimate would be the number of sites occupied over the total number of sites surveyed, i.e., $\psi = \frac{occupied}{total}$ (MacKenzie *et al.*, 2006). However, this fails to account for both detection error and drivers of species occupancy. A robust occupancy model must incorporate covariates as well as detection probability (Figure 1.2; MacKenzie *et al.*, 2006; Guillera-Arroita, 2017). Most occupancy models use a hierarchical model structure integrating two processes (Figure 1.2A): a system constituting the underlying biological system (i.e., species occupancy and the associated covariates) and the detection process (Tobler *et al.*, 2015; Guillera-Arroita, 2017). This general two-level hierarchical model accounts for the fact that the biological system is only partially available for observation due to imperfect detection (King, 2014).

Describing the biological system usually takes the form of a logistic regression which relates the probability that a species is present at a site to the associated environmental predictors through a logit link function (Figure 1.2B). The parameters related to the probability of occupancy are conditional on the underlying occupancy state. Assuming no false positive

detection (Type I error), a species cannot be detected at a site it does not occupy, while at a site that is occupied the species will be detected based on the given detection probability (Mackenzie *et al.*, 2003; MacKenzie *et al.*, 2006). Model fitting can be implemented within the frequentist (maximum-likelihood) or Bayesian frameworks.

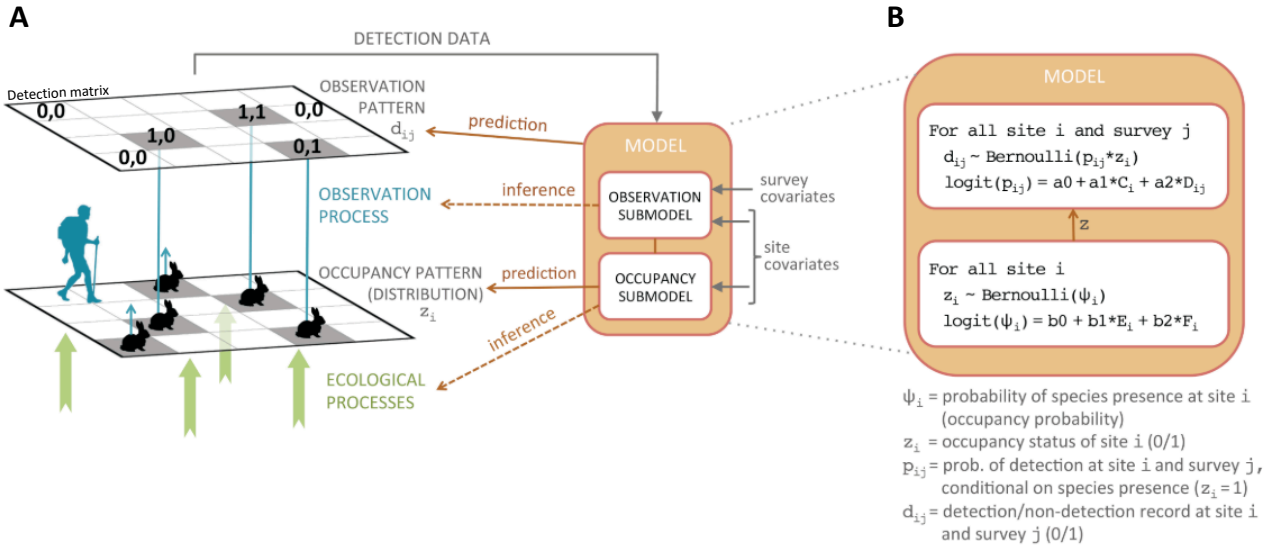

Figure 1.2 Breakdown of the data structure and modelling needs of single-species, single-season occupancy models, adapted from Guillera-Arroita (2017). **A)** An occupancy model has two components: one that describes the relationship between the chosen covariates and species occupancy, and one that describes how the observed occupancy pattern can be influenced by detection. **B)** An example of how to construct an occupancy model. The detection history is in the form of binary records d_{ij}. The presence-absence of a species at a site z_i is modelled using a logistic regression, as a function of two site level covariates: E and F. The probability of detection p_{ij} is modelled through a second logistic regression, as a function of two covariates: site-specific C, and survey-specific D.

The rise of occupancy modelling has allowed for camera trapping surveys to be used as a surrogate method for estimating abundance (Mackenzie and Royle, 2005; Ahumada *et al.*, 2011; Mordecai *et al.*, 2011). The assumptions of an occupancy model include (Mackenzie *et al.*, 2003):

1. Occupancy state is "closed". That is, the species of interest is present within the site for the duration of the survey and its occupancy does not change during the course of the sampling period.
2. Sites are independent. Detection of a species at one site is independent of detecting the species at other sites.
3. No unexplained heterogeneity in occupancy. The probability of occupancy is constant across sites or if differences in probability do occur, they can be explained by the

selected covariates included in the model.

4. No unexplained heterogeneity in detection. This is similar to assumption 3 whereby any variation in detectability between sites must be accounted for with selected covariates in the model.

New approaches to occupancy modelling are regularly being developed that allow for increased flexibility in study design (Altwegg and Nichols, 2019), relaxation of model assumptions (Gould *et al.*, 2019), the evaluation of complex relationships (e.g., species interactions; Rota *et al.*, 2016), and the ability to account for additional sources of bias (e.g., "false positive" detections associated with species misidentification; Ferguson, Conroy and Hepinstall-Cymerman, 2015). The closure assumption, assumption 1 above, is often violated with wide-ranging, territorial species that move in and out of the sample unit. However, recent studies have shown that occupancy models can still be an effective tool for studying the distribution of highly mobile species even when the assumption of geographic closure is ignored (Gould *et al.*, 2019). Although violating this assumption may not bias results, the produced estimates should be interpreted as the probability of "use" rather than occupancy (Kendall and White, 2009). Non-independence in sites can arise when sample sites are located too close to one another, allowing an individual to be detected at multiple sites simultaneously. This results in overdispersion as the true number of independent sites is smaller than the number of sites sampled and can result in overestimated abundances, potentially leading to inappropriate management decisions (MacKenzie and Bailey, 2004; Martin *et al.*, 2011). Goodness-of-fit assessments have the power to detect and adjust for this dispersion (MacKenzie *et al.*, 2006).

The last two assumptions imply that variation in occupancy and detection probability is appropriately modelled with the chosen covariates, i.e., there is no unmodeled variation. This is a typical situation in occupancy modelling, especially when analysing historical or inherited data, where the required covariates were not measured at the time. For example, carnivore occupancy is likely a function of local prey abundance or density, however, without *a priori* knowledge on these numbers this covariate cannot be confidently included in the model (Gerber *et al.*, 2009). Coarse-scale proxy variables can be used, but this may not be available or poorly represent the true distribution of the desired covariates. This unobserved detection heterogeneity can be addressed using finite mixtures, where multiple finite detection

probabilities are considered, or by incorporating a random effect, where detection probabilities are treated as a probability distribution with a mean μ and standard deviation σ (Mackenzie *et al.*, 2003; Royle and Nichols, 2003; MacKenzie *et al.*, 2006; Gerber *et al.*, 2009).

1.4 | Rationale and aims of the study

Mesocarnivores are poorly studied (du Plessis *et al.*, 2015) with most research focused on large, charismatic apex predators. They occur across ecosystems with a range of trophic pressures; from those in which large predators still persist, to others that have been completely transformed through urbanisation or agriculture (Tambling *et al.*, 2018). In South Africa, the trophic status of mesocarnivores is largely unknown and case-specific. Consequently, we know little about the conservation status of mesocarnivores both within and outside of PAs. Anecdotal evidence, such as the disappearance of black-backed jackals from Hluhluwe-Imfolozi National Park in KwaZulu-Natal (KZN) and their subsequent reintroductions and repeated demise in the 1990s (Somers *et al.*, 2017), suggest that there are serious unknown threats to mesocarnivores.

Within PAs, research opportunities on mesocarnivores are limited largely because they are not seen to be as ecologically important as their larger counterparts (Roemer, Gompper and Van Valkenburgh, 2009) and are less likely to attract funding or interest from tourists. To circumvent this, one can leverage research efforts on larger carnivores to study mesopredators within PAs. Thus, a camera trap survey designed to monitor apex predator abundance can provide useful data on mesocarnivores. Although these surveys may not be optimized for mesocarnivore research, largely due to camera placement, the data are still potentially valuable for exploring mesocarnivore presence within PAs.

In this study I use data collected as part of a large-scale project on leopard density within PAs in KZN to explore variation in mesocarnivore presence and richness. I selected seven PAs that range in size, management history and surrounding land-use. I aim to test the hypothesis that mesocarnivore habitat use and richness within PAs is influenced by a broad range of environmental and anthropogenic variables. These variables include the presence of larger predator species, vegetation characteristics, terrain complexity and human disturbance

surrounding the PA. Collecting data over a variety of PAs allowed me to investigate possible reasons for observed mesocarnivore population distributions within PAs. Additionally, gaining a baseline of information on the current population status can allow for better management of mesocarnivore species in these areas, especially under continued habitat change and persecution.

2 | METHODS

I adopt occupancy nomenclature, in which "site" refers to the selected PA in which the surveys occurred. "Survey" defines a continuous primary sampling period within the site in a given year. The survey period is subdivided into a number of secondary sampling "occasions" over which sampling is replicated, and finally, "station" defines the location of a pair of camera traps.

2.1 | Study areas

Camera surveys were conducted as part of Panthera's national leopard monitoring programme, established to monitor leopard population status across South Africa. The programme started in 2013 and has expanded through time such that a total of 20 PAs were surveyed in 2018. This study utilized a subset of the camera trap data collected from seven PAs distributed across northern KwaZulu-Natal (KZN), South Africa in 2015 (Figure 2.1). All seven sites are classified as "Nature Reserves" (Protected Areas Act 57, 2003). These sites included the Eastern Shores Section of iSimangaliso Wetland Park (Eastern Shores), Hluhluwe-Imfolozi Park (HiP), Ithala Game Reserve, Somkhanda Game Reserve, Tembe Elephant Park, uMkhuze Game Reserve and Zululand Rhino Reserve (ZRR). Management authorities varied between sites (Table 2.1) and included provincial (n = 5), community (n = 1) and private (n = 1) PAs. Sites were on average 377 $\pm$ 236 km^2 in size and collectively covered 2643 km^2 (Table 2.1).

Zululand Lowveld vegetation was the dominant vegetation type within three of the study sites, namely HiP, Somkhanda and ZRR. Dominant vegetation in the other sites included Tembe Sandy Bushveld (Tembe), Western Maputaland Clay Bushveld (uMkhuze), Ithala Quartzite Sourveld (Ithala) and Subtropical Freshwater Wetlands (Eastern Shores) (Table A3).

Figure 2.1. Land-use map of the study area in northern KZN, South Africa. Camera stations (+) were located in seven study sites/PAs: (1) Eastern Shores (n = 41 camera stations) sampled between September and November 2015, (2) HiP (n = 46) sampled between May and June 2015, (3) Ithala (n = 31) between March and June 2015, (4) Somkhanda (n = 41) between January and March 2015, (5) Tembe (n = 32) between July and August 2015, (6) uMkhuze (n = 40) between June and July 2015, and (7) ZRR (n = 40) between July and September 2015. Numbers correspond with Table 2.1.

Table 2.1 The names and size of the seven study sites located in northern KZN, South Africa. Camera surveys were conducted as part of Panthera's 2015 leopard monitoring programme. "Site" refers to the selected PA in which the survey occurred, "station" defines the location of a pair of camera traps and "occasions" are the number of secondary sampling periods. Bold numbers correspond with Figure 2.1.

	Site name	Area (km^2)	No. of stations	Start date	End date	No. of occasions*	Season	Management authority
1	Eastern Shores Section of iSimangaliso Wetland Park	264	41	25/09/2015	08/11/2015	1832	Dry/Wet	Provincial
2	Hluhluwe-Imfolozi Park	904	46	01/05/2015	14/06/2015	2045	Dry	Provincial
3	Ithala Game Reserve	292	31	29/03/2015	12/05/2015	1349	Wet	Provincial
4	Somkhanda Game Reserve	313	41	30/01/2015	15/03/2015	1737	Wet	Community
5	Tembe Elephant Park	299	32	12/07/2015	25/08/2015	1392	Dry	Provincial
6	uMkhuze Game Reserve	355	40	02/06/2015	16/07/2015	1759	Dry	Provincial
7	Zululand Rhino Reserve	216	40	29/07/2015	11/09/2015	1793	Dry	Private

*camera occasions were calculated by summing all days the camera stations were active

2.2 | Study species

Table 2.2 The common and scientific names of the five mesocarnivore species included in my study in addition to the average adult body mass, calculated from Hunter and Barrett (2011), IUCN conservation status taken from IUCN (2019) and the South African status taken from Friedmann and Daly (2004). LC - Least concern and NT - Near threatened.

Common name	Scientific name	Average adult body mass (kg)	IUCN status	South African status
Caracal	*Caracal caracal*	14	LC	LC
Side-striped jackal	*Canis adustus*	13	LC	NT
Black-backed jackal	*Canis mesomelas*	13	LC	LC
Honey badger	*Mellivora capensis*	11	LC	NT
Serval	*Leptailurus serval*	11	LC	NT

All five mesocarnivore species included in the study (Table 2.2) are thought to be widespread throughout South Africa. Black-backed jackals and caracals are ubiquitous in agricultural areas and, as a result are commonly persecuted. The other three species are also associated with livestock predation, though to a lesser degree (Kerley *et al.*, 2018). Therefore, understanding the presence of these agricultural 'pest' species in PAs is important for their overall management (Turpie and Babatopie, 2018).

2.3 | Camera trap survey design

Within each site, 31-46 paired camera trap stations were deployed for approximately 45 ± 2 days (Table 2.1, Figure 2.1). Stations consisted of a pair of unbaited, heat-in-motion triggered PantheraCam V-series camera traps with passive infrared sensors (Figure 2.2; Olliff *et al.*, 2014) positioned approximately 40 cm above the ground on trees or steel poles. Stations were spaced 1-3 km apart so as to maximise the probability of detecting Panthera's target species, leopards (Tobler and Powell, 2013). This distancing has also been shown to be appropriate for monitoring multiple medium- to large-sized mammals in forest and savanna/grassland systems (O'Brien *et al.*, 2010). Cameras were set alongside publicly-accessible roads, management tracks, drainage lines and well-used animal paths to optimise detection probabilities (Figure 2.2 and Figure 2.3). Cameras were placed opposite each other on either side of the track but not facing each other directly (offset by ~2 m) to avoid camera flash reflection. Each station was treated as a single data point by combining detections from the two opposing cameras using the time/date stamps recorded (e.g., if a caracal was

recorded by both cameras and shared a date/time stamp, it was recorded as a single detection). Independent captures were defined as photo events separated by ≥30 minutes unless different individuals could be distinguished. Finally, to minimise false detections, vegetation around each individual camera that might obstruct the camera's field of view was cleared. Camera traps were not moved during the individual surveys. Cameras were checked every 7-10 days to replace batteries, download images and perform any other maintenance tasks that were required. Camera settings included medium trigger sensitivity, with a flash distance of ~5 m (Figure 2.3). When flash was employed for nocturnal captures, a single image was taken per trigger with an 8 second delay between each image. When flash was not used, 3 daylight images were captured per trigger with a 0.3 second delay between each image.

A detection history was then created for each individual species based on the date and location of individual captures. For each site, the observed data consisted of an $M \times J$ matrix where M was the number of stations and J was the number of occasions. A camera station was considered to be active if at least one of the two cameras was operational. For each occasion, the species was either registered as detected ("1") or not detected ("0"). The occasion matrix was later pooled into 5-day occasion periods to reduce zero-inflation and improve model fit.

Figure 2.2 PantheraCam V-series camera trap (insert) and mounted on metal pole along an animal track.

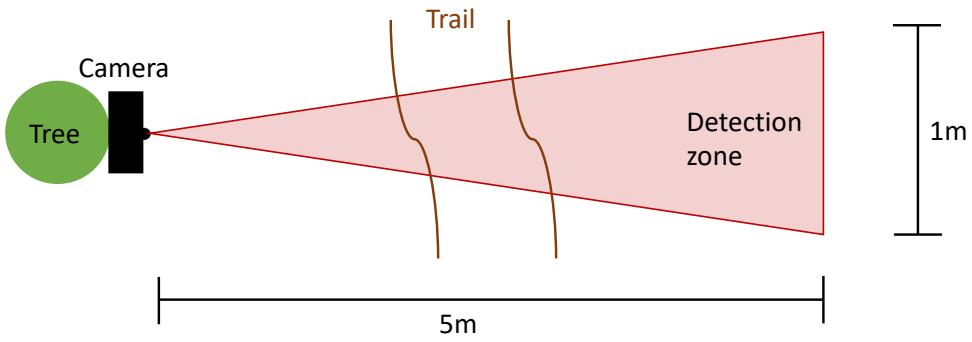

Figure 2.3 Schematic showing the detection zone of a PantheraCam V-series camera trap mounted on a tree and placed along an animal trail.

2.4 | Occupancy model covariates

2.4.1 | Protected Area (PA)

There are many aspects of a PA that are difficult to measure, or are unknown, such as its land-use history, past and current management, or disease outbreaks. Additionally, surrounding land-use, and exposure to human disturbance, varied around the different PAs (Figure 2.1). Therefore, PA was included as a covariate to try and incorporate some of this variation into the final model.

2.4.2 | NDVI

Increased habitat closure was thought to increase mesocarnivore habitat use, as it provides refugia for smaller, less-dominant species (Roemer, Gompper and Van Valkenburgh, 2009; Wilson *et al.*, 2010). Vegetation primary productivity was estimated using the Normalised Difference Vegetation Index (NDVI), computed as:

$$\frac{NIR - red}{NIR + red}$$

where NIR is the amount of near-infrared light and red is the amount of red light reflected by a surface and measured by a satellite sensor (Pettorelli *et al.*, 2011). Plant material generally has high visible light absorption and high near-infrared reflectance, thus resulting in positive NDVI values that represent photosynthetic activity and canopy structure (Pettorelli *et al.*, 2005, 2010). NDVI has been found to decrease as vegetation becomes more open (e.g., forest to grassland; Martinuzzi *et al.*, 2008). NDVI observations were acquired from the Tera

MODIS MOD13A1 Version 6 dataset (Huete *et al.*, 2002). NDVI was sampled on a pixel scale every 16 days at 500 m resolution. NDVI within a 1 km buffer area around each station was averaged and values were limited to periods encapsulating the respective survey period of approximately 45 days (Table 2.1).

2.4.3 | Terrain complexity

Water availability is difficult to measure as many satellite or aerial methods cannot account for all forms of "available water", such as many temporary water sources, soil moisture and groundwater (Rockström *et al.*, 2009; Gerten *et al.*, 2011). Multiple surveys in this study were conducted over wet seasons where temporary water sources would have been prevalent. Terrain complexity can reflect hydrological profiles and also influence availability of refuge and foraging diversity, ultimately impacting prey densities (Berryman *et al.*, 2015). Therefore, it was thought that terrain complexity may be a more important variable than distance to water. Terrain complexity has also been shown to be important in estimating the occupancy of black-backed jackals and caracals (Drouilly, Clark and O'Riain, 2018); therefore, I hypothesised that mesocarnivore habitat use would increase in areas with greater terrain complexity. Terrain complexity is a convoluted factor, and difficult to quantify; thus, the Terrain Ruggedness Index (TRI) was used as a proxy variable (Pitman *et al.*, 2017). TRI was derived from 30 m resolution Shuttle Radar Topography Mission (SRTM) elevation data (USGS, 2014). Each pixel was rescaled to 500 m and calculated as the square root of the summed squared difference of a pixel and its eight neighbours. TRI at each station was then calculated as the average TRI within a 1 km buffer area around each station.

2.4.4 | Distance to PA edge

Reduction and/or degradation due to human presence around PAs can greatly reduce its overall health and functional size. Additionally, these edge effects can lead to population sinks from illegal poaching, introduction of invasive species and diseases, or increased human-wildlife conflict (Woodroffe and Ginsberg, 1998; Massey, King and Foufopoulos, 2014). Therefore, I hypothesised that mesocarnivore habitat use and species richness would decrease closer to the edges of PAs. An alternative hypothesis is that, as a population sink, the edges could have increased species richness and habitat use, particularly with

mesocarnivores utilising invasive animals from the anthropogenically manipulated peripheries and generalist mesocarnivores moving from the PA source/core. Distance to the edge of the PA was used as a proxy for these hypothesised edge effects. Spatial polygons for each PA were aggregated from land owners, PA management and the World Database on Protected Areas (IUCN and UNEP-WCMC, 2019). Distance to the edge was then calculated as the linear distance from a camera station to the nearest point outside of the PA.

2.4.5 | Domestic dogs

As domestic dogs generally occur in close proximity to human-dominated areas (Silva-Rodríguez and Sieving, 2012), it was thought that the presence of domestic dogs within a PA would be a good proxy for human disturbance bordering the PA , as well as the permeability of the surrounding fence structure. Additionally, dogs are often used in bushmeat hunting (Jachmann, 2008; Grey-ross, Downs and Kirkman, 2010; Lindsey *et al.*, 2011), and thus could also reflect poaching pressure within the PAs. It was hypothesised that both mesocarnivore habitat use and richness would decrease with increased domestic dog abundance due to direct competition and disease risk (Zapata-Ríos and Branch, 2018). Domestic dog relative abundance (hereafter referred to as "dogs") was estimated using Relative Abundance Indices (RAI), where total independent ($\geq$30 min) dog detections were summed for each station, standardised by effort, i.e., the number of days the station was active/operational, and multiplied by 100.

2.4.6 | Apex predators

It was thought that interspecific predation and competition would play a major role in determining mesocarnivore habitat use and richness (Fuller, 1996). Large carnivores, such as leopard, lion (*Panthera leo*) and spotted hyaena (*Crocuta Crocuta*), often prey upon smaller carnivores such as caracal, honey badger (*Mellivora capensis)* and jackal species, and can significantly shape mesocarnivore communities through direct mortality and induced avoidance behaviour (Hayward *et al.*, 2006; Ramesh, Kalle and Downs, 2017b). I hypothesised that mesocarnivores would be more successful, that is have increased habitat use and species richness, with reduced apex predator abundance (Drouilly *et al.*, 2018). An alternative hypothesis is that apex carnivores facilitate mesocarnivores by providing scavenging

opportunities (Kowalczyk *et al.* 2008; Sivy *et al.* 2017; Wilmers *et al.* 2003), and so increased habitat use and species richness would be expected with increased apex predator abundance or *vice versa*. Apex predator RAI was calculated in the same way as domestic dogs where the total number of independent apex carnivore detections were summed across species (leopard, lion and spotted hyaena) and stations, standardised by effort, and multiplied by 100. It must be noted that the roles of apex predators vary with size, hunting strategy and social structure, and so the amalgamation of "apex carnivores", while necessary for all species other than leopards due to small sample sizes, may conflate apex influences on mesocarnivores.

2.5 | Detection covariates

Positioning of cameras by landscape features such as roads, animal tracks and/or river beds, hereafter referred to as "trail", was included as a detection factor as this may have favoured the detection of some mesocarnivore species over others. Due to the variety of dominant vegetation located within each study site (Table A3), PA was also included as a detection covariate.

2.6 | Multi-species Royle-Nichols occupancy model (RN)

As previously mentioned, occupancy models provide an estimate of occupancy (ψ), i.e., the probability that the study site is occupied by a particular species during the survey period (Mackenzie *et al.*, 2002). As my study dealt with highly-mobile species, with male black-backed jackals having an average home range of 18.2 km^2 within a KZN PA (Rowe-Rowe, 1982) and 288.5 km^2 for male caracals in KZN agricultural landscape (Ramesh, Kalle and Downs, 2017a), sampling unit closure could not be assumed (assumptions outline on page 17), and thus the model outputs were interpreted as the probability that a species "uses" a site, rather than the traditional occupancy probability. Despite violating the assumption that sampling units are independent, occupancy models are still an effective tool in estimating habitat use of highly-mobile species (Gould *et al.*, 2019). For the model to accurately estimate habitat use, imperfect detection and covariates thought to influence both use and detection must be incorporated (Reilly *et al.*, 2017).

Tobler *et al.* (2015) developed a multi-species extension of the Royle-Nichols (RN) occupancy model (Royle and Nichols, 2003) that utilizes camera trap detection data to monitor a variety of species compositions and occupancy over time. The basic single-species Royle-Nichols model estimates occupancy rate or the proportion of area used as a function of species abundance. The model assumes that variations in abundance will induce variation in detection probability (Royle and Nichols, 2003). Therefore, their method estimates species abundance from repeat observations of the presence-absence of a species, without requiring individual identification. The multi-species extension of this model allows for multiple species abundances to be estimated and allows multiple study areas to be compared, while still accounting for species-specific differences in detection. I adapted this multi-species RN model to analyse how different PAs, as well as human disturbance and environmental covariates affect species-level and guild-level mesocarnivore habitat use.

2.6.1 | Model framework

The theoretical background of my model follows Tobler *et al.* (2015) closely, while model specifics were obtained from Li, Bleisch and Jiang (2018). w_{il} was defined as a latent binary variable that indicated whether the species of interest i was present $(w_{il} = 1)$ or absent $(w_{il} = 0)$ in the PA l. It was assumed that w_{il} was a Bernoulli random variable and governed by the hyperparameter[5] Ω_i, where Ω_i is a rate between 1 and 0 indicating the proportion of sites where species i was present.

$$w_{il} \sim Bernoulli(\Omega_i)$$

Ω_i can also be thought of as habitat use at the PA level, this is important as it allows some species to be completely absent from certain PAs. The observed occurrence state of species i at camera station j was defined by the binary variable z_{ij} where:

$$z_{ij} \sim Bernoulli\big(w_{il} \times \psi_{ij}\big),$$

where ψ_{ij} is the probability that species i uses the area around station j.

[5] A hyperparameter is a parameter whose value is based off a prior distribution (Riggelsen, 2006). For example, if the variance parameter τ^2 has a uniform prior of (0, θ), then τ^2 is a parameter (in the distribution of the data) and θ is a hyperparameter, as it is not based on observed data.

The RN model estimates the abundance distribution of species i using the probability of habitat use, such that:

$$\psi_{ij} = \Pr(a_{ij} > 0) = 1 - \exp(-\lambda_{ij})$$

Where the abundance of species i at station j (a_{ij}) is modelled as a random Poisson variable λ_{ij};

$$a_{ij} \sim Poisson(\lambda_{ij}),$$

It was hypothesized that mesocarnivore habitat use would vary with ecological and anthropogenic covariates (COV: NDVI, TRI, distance to PA edge, domestic dog and apex predator abundance) and across all PAs.

Thus, the expected abundances (λ_{ij}) were calculated as:

$$\log(\lambda_{ij}) = \beta_{0i} + \sum_{x}^{n=5} \beta_{xi} COV_x + \beta_{6i} PA_j$$

where x is the index of the five covariates. Individual detection probabilities varied with PA and trail:

$$logit(p_{ij}) = \alpha_{0i} + \alpha_{1i} trail_j + \alpha_{2i} PA_j$$

All continuous covariates were standardized to have a mean of zero and a standard deviation of one.

Following Reilly *et al.* (2017) and Li, Bleisch and Jiang (2018), species-level parameters were modelled as random variables drawn from a normal distribution with a mean of zero and variance (σ^2) described by community hyperparameters, e.g., $\beta_{1i} \sim Normal(0, \sigma^2)$. This was done to improve parameter estimations for scarcely detected species. Following Rich *et al.* (2016) all species were pooled into a "community", with all species richness estimates being derived from the community model with community-level hyperparameters.

Modelling was carried out in a Bayesian framework using BUGS (Bayesian inference Using Gibbs Sampling) language and run in JAGS (Just Another Gibbs Sampler) software (Plummer, 2003; version 3.4.0) with the R package R2Jags (Su and Yajima, 2015; version 0.5-7). Vague, independent priors were derived from normal prior distributions (mean = 0 and standard deviation = 1000) for the community-level habitat use and detection covariates. The posterior distribution was obtained by running 3 chains of The Markov Chain Monte Carlo (MCMC),

with 140 000 iterations, a burn-in of 100 000 iterations and a thinning rate of 40. Therefore, final inferences were made from a sample size of 3 000, and deemed adequate based off later $\hat{R}$ statistics (Gelman and Rubin, 1992). In some settings, thinning does not help with convergence and could be inefficient (Link and Eaton, 2012). Unfortunately, high autocorrelation in my model was unavoidable; thus, requiring very long chains. With multiple nodes being monitored, computer memory and storage was a major limitation, and therefore, resulting in a high burn-in and thinning rate to reduce this cost (Broms, Hooten and Fitzpatrick, 2016). Additionally, due to substantial post-processing required, whereby derived parameters were calculated for each sampled value of the Markov chain, posing a substantial computational burden, it was thought that overall results would be improved by reducing autocorrelation in the chains being used through increased thinning (Link and Eaton, 2012).

2.6.2 | Candidate models

To avoid the risk of model over-parameterization that could reduce the precision of the habitat use estimates, only a few hypotheses driven models were considered. These models explored three broad drivers of mesocarnivore habitat use, namely:

1. Environmental drivers: NDVI and TRI
2. Interspecific drivers: Competition/predation from apex predators and domestic dogs
3. Anthropogenic drivers: Distance to PA edge and domestic dogs

A global model, incorporating all the above covariates, was also examined. Due to the survey being designed for monitoring leopards, and leopards being detected across all surveyed PAs, a second set of global and competition models were also considered, exploring the influence of leopard relative abundance rather than just apex predator abundance as a whole. Finally, a null model, which only incorporated detection covariates, was considered.

2.6.3 | Model fit assessment

Convergence was assessed visually by inspecting the produced MCMC chains and using the Gelman-Rubin statistic, where $\hat{R} < 1.1$ was considered to be acceptably converged (Gelman and Rubin, 1992; Brooks and Gelman, 1998). “Lack of fit” of the data was evaluated using the Bayesian p-value (Kéry, 2010), a posterior-predictive check that estimates the level of

dispersion in the data relative to the model. The Bayesian p-value is defined as the probability that the replicated data are more extreme than the observed data. The Bayesian p-value was estimated based on the Pearson's χ^2 discrepancy for binomial data, such that $\Pr(\chi^2_{obs} > \chi^2_{sim})$. The simulated data were assumed to be "perfect", and thus allowing the Pearson residuals to represent the fit of the model when all model assumptions were perfectly met (Kéry, 2010). This created a fit metric that was equal to one when the Pearson residual was greater for the observed data than the simulated data, or equal to zero otherwise. Therefore, the final Bayesian p-value was calculated as the mean of the posterior sample of the model fit metric, where a mean of 0.5 indicated perfect fit, and values between 0.05 and 0.95 indicated adequate model fit (Soto-Shoender *et al.*, 2018). Finally, a "lack-of-fit" statistic was reported $\frac{\chi^2_{obs}}{\chi^2_{sim}}$, which was expected to equal 1 when the data fit the model perfectly (Kéry and Schaub, 2012).

2.6.4 | Derived parameters

Many occupancy models can estimate the number of species in a community that were unobserved during the sampling period (Guillera-Arroita, Kéry and Lahoz-Monfort, 2019), but this often requires prior knowledge of the total number of species that can possibly occur at a site. However, there was no well-documented mesocarnivore species list for all the PAs considered in my study. Due to this, I could not derive absolute species richness, but instead focused on comparing the relative species richness of focal mesocarnivore communities in the different PAs.

The probability that a species was present during a survey, but not detected, was calculated using MCMC algorithms, where $w_{il} = 1$ for each iteration if the species was detected during the survey. If the species was not detected, then a mean of w_{il} was taken over all iterations. This produced a probability that the species was present but overlooked, while also taking into account the probability of habitat use of the species, PA, sampling effort and detection probability across surveys.

The total number of species present during each survey l, or estimated species richness (s_l), was calculated as:

$$s_l = \sum_i w_{il}$$

Station-level species richness was then estimated using a similar occurrence matrix as above, adapted to the station-level, where species of interest i was present ($z_{ij} = 1$) or absent ($z_{ij} = 0$) in the area around station j. Species richness per station was calculated as $s_j = \sum_i z_{ij} w_{il}$.

2.7 | Species richness - Generalized Additive Model

Generalized Additive Models (GAMs) are flexible models and can be used to maximize the predictive quality of a covariate from various distributions, and thus allowing for better fit in the presence of non-linear relationships and significant noise in the predictor covariates (Hill and Lewicki, 2007). GAMs are often used to predict the likelihood of species presence and abundance using environmental variables and have been shown to perform better than other types of ecological predictive models (Guisan, Edwards and Hastie, 2002; Moisen and Frescino, 2002). In my study, GAMs were applied to model the relationship between station-level species richness and various predictor covariates.

General GAMs are expressed as:

$$g(\mu) = \alpha + \sum_{i=1}^{n} f_i(x_i) + \varepsilon$$

where $g(\mu)$ is the link function defining the relationship between the response variable (species richness) and the predictor variables (selected covariates). α is the intercept term, n the number of covariates, f_i is the spline smoothing function of each predictor x_i, and ε is the residual error term (Wood, 2017). Thin plate regression splines were used as the smoothing function for all covariates. This approach allowed lower ranked smooths to be nested within higher ranked smooths, thus allowing conventional hypothesis testing methods to be used to compare GAMs (Wood, 2003). Four GAMs were developed based on the candidate models outlined for the RN model, namely, 1) Environmental: NDVI and TRI, 2) Anthropogenic: Distance to PA edge and domestic dog abundance, and 3) Competition:

domestic dog and leopard abundance. The global GAM was based on the best-fit RN model (Global B, Table 3.3), i.e., 4) Global: NDVI, TRI, distance to edge, dogs and leopard abundance. The best-fitting GAM was selected based on the Akaike's Information Criterion (AIC; Sagarese *et al.*, 2014). A fifth GAM was also developed using the second best-fit RN model (Global A; Table 3.3). All GAMs were run using the R package 'mgcv' (Wood, 2011; version 1.8-28).

2.8 | Species richness - Variance model

In order to assess the effects of each variable on the variation in species richness, I used a log-linear regression of the variance in species richness on all covariates (Kéry, 2010; Li, Bleisch and Jiang, 2018). Species richness for station i was drawn from a normal distribution with mean (μ_i) and variance ($^1/_\sigma$).

The variance (χ) of the x covariates (COV), namely, NDVI, TRI, distance to PA edge, dog and leopard abundance, was then calculated using:

$$\log(\sigma_i) = \chi_0 + \sum_{x}^{n=5} \chi_x COV_x$$

Where σ_i is the variance in species richness for station i, and χ_0 is the mean variance drawn from a normal distribution with mean of zero and a variance of 0.001.

This modelling process was also carried out in R2Jags (Su and Yajima, 2015; version 0.5-7), using uninformative priors derived from normal prior distributions with mean zero and variance 0.001. The posterior distribution was obtained by running 3 chains of MCMC with 20 000 iterations, a burn-in of 10 000 iterations and a thinning rate of 10.

3 | RESULTS

3.1 | Descriptive results

A total of 392 642 photographs were collected over 13 823 trap nights for the seven camera trap surveys (Table 3.1). The number of trap days were similar (1689 $\pm$ 230 days) across all surveys. Duplicates, 'blank' photos and photos of the research team accounted for 137 966 of the photographs and were removed prior to analyses. Independent captures were broken down into a total of 64 species across 14 orders (including human unknown and "other" photographs; Table 3.2). ZRR produced captures of the greatest number of species, whilst Tembe the least (Table 3.1).

The total number of detections for the five mesocarnivores species varied markedly across the different PAs (Table 3.2). Honey badger was the only species detected across all surveyed PAs, while serval was detected in five PAs, side-striped jackals in four, black-backed jackals in three and caracal in two of the PAs. When comparing PAs, ZRR was the only PA in which all five mesocarnivores were detected (Table 3.2). The highest number of mesocarnivore detections were recorded for ZRR (N = 117). Detections of black-backed jackal, honey badger and serval were distributed evenly throughout ZRR (Figure 3.4). By contrast, Tembe had the lowest number of detections across all focal species with honey badger being the only mesocarnivore detected (N = 8). These detections were mostly confined to the southern regions of Tembe (Figure 3.2). Eastern Shores had the highest number of a single mesocarnivore species, honey badger, detected (N = 62; Table 3.2). These detections occurred mostly along the eastern boundary of the PA, close to the ocean (Figure 3.1; Figure 2.1). The highest number of detections for side-striped jackal occurred in uMkhuze and appeared to be evenly spread throughout the surveyed area (Figure 3.3). HiP had the second lowest total number of mesocarnivore detections (N = 10), however these were spread over three species, namely honey badger, side-striped jackal and serval (Table 3.2). All detections of side-striped jackal and serval in HiP occurred at a single camera station (Figure 3.3).

Table 3.1 Summary of the camera trap surveys conducted in seven PAs in KZN, South Africa, namely Eastern Shores Section of iSimangaliso Wetland Park (E.Shores), Hluhluwe-Imfolozi Park (HiP), Ithala Game Reserve, Somkhanda Game Reserve, Tembe Elephant Park, uMkhuze Game Reserve and Zululand Rhino Reserve (ZRR). Area is the total area (km^2) covered by the camera trap stations. Trap days is the total number of days cameras were active at each site, independent captures refers to the total number of independent photographs ($\geq$ 30 min) of target species and total species is a count of the total number of different animal species (domestic and wildlife) detected by that camera trap survey.

PA	Area	No. of stations	Total trap days	Total no. of captures	Independent captures	Total species
E.Shores	148	41	1834	114705	83169	41
HiP	336	46	1957	93495	62438	44
Ithala	236	31	1349	36864	21065	45
Somkhanda	229	40	1739	23310	13460	44
Tembe	166	32	1392	42714	21863	40
uMkhuze	146	40	1759	51524	36856	45
ZRR	200	40	1793	30030	15825	48

Table 3.2. Summary of the number of captures of the 64 species detected for 1-day occasion periods (i.e., before pooling) across the seven PAs in KZN, South Africa, namely Eastern Shores Section of iSimangaliso Wetland Park (E.Shores), Hluhluwe-Imfolozi Park (HiP), Ithala Game Reserve, Somkhanda Game Reserve, Tembe Elephant Park, uMkhuze Game Reserve and Zululand Rhino Reserve (ZRR). Mesocarnivores considered in this study in bold.

Species	Common name	E.Shores	HiP	Ithala	Somkhanda	Tembe	uMkhuze	ZRR
Carnivora								
Acinonyx jubatus	Cheetah	0	1	0	0	0	19	14
Aonyx capensis	Cape Clawless Otter	0	0	1	0	0	0	0
Atilax paludinosus	Water Mongoose	45	1	4	3	6	1	1
Canis adustus	**Side-striped Jackal**	**13**	**1**	**0**	**0**	**0**	**35**	**11**
Canis mesomelas	**Black-backed Jackal**	**0**	**0**	**5**	**10**	**0**	**0**	**46**
Caracal caracal	**Caracal**	**0**	**0**	**0**	**8**	**0**	**0**	**4**
Crocuta crocuta	Spotted Hyaena	334	407	6	38	1	165	34
Felis serval	**Serval**	**21**	**3**	**26**	**11**	**0**	**0**	**34**
Galerella sanguinea	Slender Mongoose	0	2	14	10	10	3	1
Genetta tigrina	Large-spotted Genet	62	31	57	56	110	100	38
Hyaena brunnea	Brown Hyaena	0	0	75	5	0	0	43
Ichneumia albicauda	White-Tailed Mongoose	4	43	42	54	44	103	88
Ictonyx striatus	Striped Polecat	0	0	0	0	15	0	0
Lycaon pictus	Wild Dog	0	109	0	154	45	147	50
Mellivora capensis	**Honey Badger**	**62**	**6**	**14**	**5**	**8**	**11**	**22**
Mungos mungo	Banded Mongoose	9	0	0	0	2	7	2
Panthera leo	Lion	0	124	0	0	197	49	118
Panthera pardus	Leopard	217	121	359	58	102	115	88
Rhynchogale melleri	Meller's Mongoose	0	0	1	0	0	1	0
Lagomorpha								
Lepus saxatalis	Scrub Hare	1	69	96	18	40	260	161

Table 3.2. (*Continued*)

Species	Common name	**E.Shores**	**HiP**	**Ithala**	**Somkhanda**	**Tembe**	**uMkhuze**	**ZRR**
Perissodactyla								
Ceratotherium simum	White Rhinoceros	24	582	123	74	28	258	189
Diceros bicornis	Black Rhinoceros	11	51	66	20	6	37	36
Equus quagga	Plains Zebra	245	446	947	298	32	510	434
Primates								
Cercopithecus albogularis	Samango Monkey	71	3	0	0	48	0	0
Cercopithecus pygerythus	Vervet Monkey	350	54	468	1295	44	386	248
Otolemur crassicaudatus	Greater Bushbaby	0	0	3	0	2	2	1
Papio ursinus	Chacma Baboon	88	186	1281	3	0	333	35
Proboscidae								
Loxodonta africana	African Elephant	8	609	207	70	634	75	164
Rodentia								
Hystrix africaeaustralis	Cape Porcupine	232	30	149	205	123	104	278
Thryonomys swinderianus	Cane Rat	0	11	2	8	0	4	2
Ruminantia								
Aepyceros melampus	Impala	37	169	422	1570	595	2809	1562
Alcelaphus buselaphus	Red Hartebeest	0	0	2	1	0	0	0
Cephalophus natalensis	Red Duiker	1441	15	1	132	398	167	131
Connochaetes taurinus	Blue Wildebeest	43	72	267	601	61	708	540
Damaliscus lunatus	Tsessebe	0	0	1	0	0	0	0
Giraffa camelopardalis	Giraffe	0	349	262	150	215	238	552
Kobus ellipsiprymnus	Waterbuck	656	39	101	39	6	0	88
Neotragus moschatus	Suni	0	0	0	0	13	5	0
Oreatragus oreotragus	Klipspringer	0	0	3	0	0	0	0

Table 3.2. (*Continued*)

Species	Common name	E.Shores	HiP	Ithala	Somkhanda	Tembe	uMkhuze	ZRR
Ruminantia								
Potamochoerus porcus	Bushpig	77	19	68	43	1	31	13
Raphicerus campestris	Steenbok	0	0	0	4	0	10	0
Redunca arundinum	Common Reedbuck	30	0	1	0	1	0	32
Redunca fulvorufola	Mountain Reedbuck	0	0	1	19	0	0	22
Sylvicapra grimmia	Common Duiker	26	99	30	130	207	238	95
Syncerus caffer	African Buffalo	340	407	9	189	4	57	196
Taurotragus oryx	Eland	0	0	48	0	0	0	0
Tragelaphus angasii	Nyala	72	332	98	1110	3037	2290	2268
Tragelaphus scriptus	Bushbuck	719	14	323	182	18	2	46
Tragelaphus strepsiceros	Kudu	736	82	765	393	72	180	582
Squamata								
Varanus species	Monitor lizard	1	1	0	0	0	0	0
Suiformes								
Hippopotamus amphibious	Hippopotamus	639	8	0	39	7	145	14
Phacochoerus africanus	Warthog	539	382	353	2194	70	862	1901
Testudines								
Geochelone pardalis	Leopard Tortoise	0	0	1	0	0	0	0
Tubulidentata								
Orycteropus afer	Aardvark	70	7	29	93	0	19	44

Table 3.2. (*Continued*)

Species	Common name	E.Shores	HiP	Ithala	Somkhanda	Tembe	uMkhuze	ZRR
Domestic								
Bos taurus	Cow	0	0	0	299	0	0	0
Canis familiaris	Dog	8	1	6	36	1	15	32
Capra aegagrus	Goat	0	0	0	0	0	0	1
Equus ferus	Horse	3	1	0	0	0	0	0
Felis catus	Cat	1	0	0	0	0	1	0
Human								
Homo sapien	Human[a]	2077	254	568	545	153	268	242
	Vehicle	73620	57032	13384	2884	15366	25843	5444
Other								
	Bat species	1	3	0	1	1	8	6
	Bird species	155	66	197	293	80	115	257
	Insect species	19	25	38	31	2	0	3
	Unknown	7	169	45	31	0	98	0

[a] Excluding research team

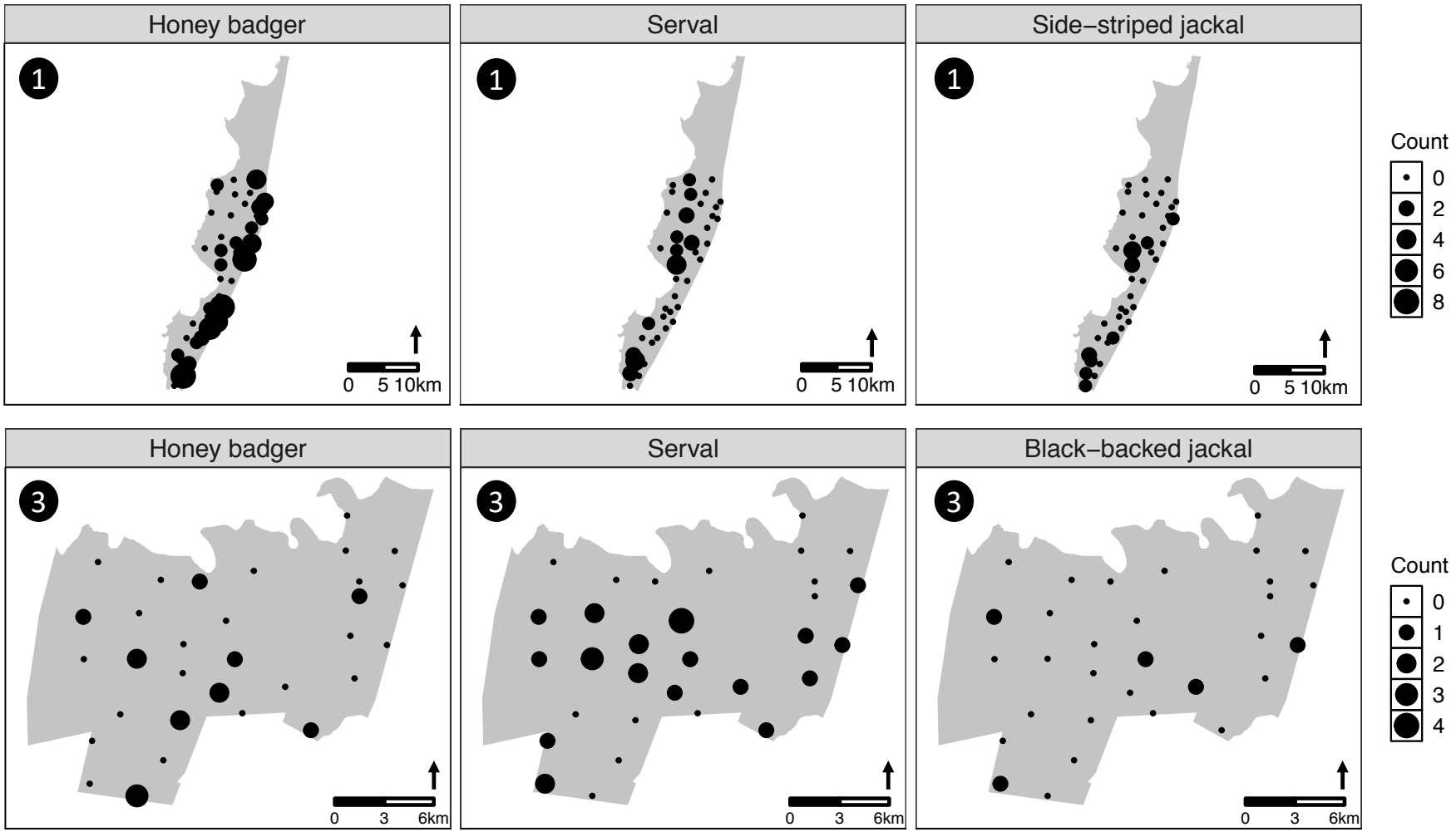

Figure 3.1 Mesocarnivore capture frequencies recorded at camera trap stations in 1) Eastern Shores Section of iSimangaliso Wetland Park (Eastern Shores) and 3) Ithala Game Reserve during 2015 surveys. Numbers correspond to survey number in Figure 2.1. Points represent station locations scaled by the number of independent captures (counts) of that species.

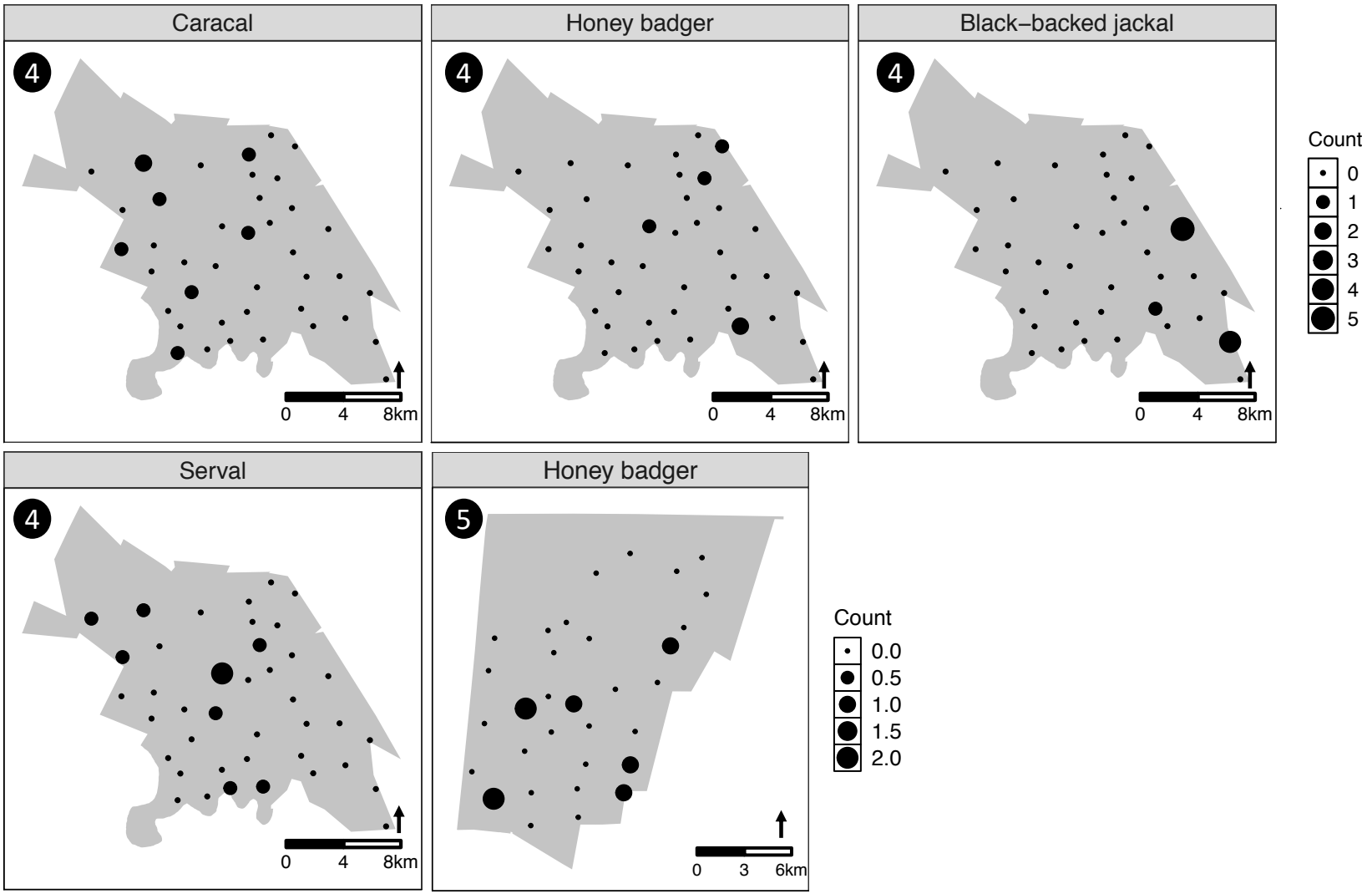

Figure 3.2 Mesocarnivore capture frequencies recorded at camera trap stations in 4) Somkhanda Game Reserve and 5) Tembe Elephant Park during 2015 surveys. Numbers correspond to survey number in Figure 2.1. Points represent station locations scaled by the number of independent captures (counts) of that species.

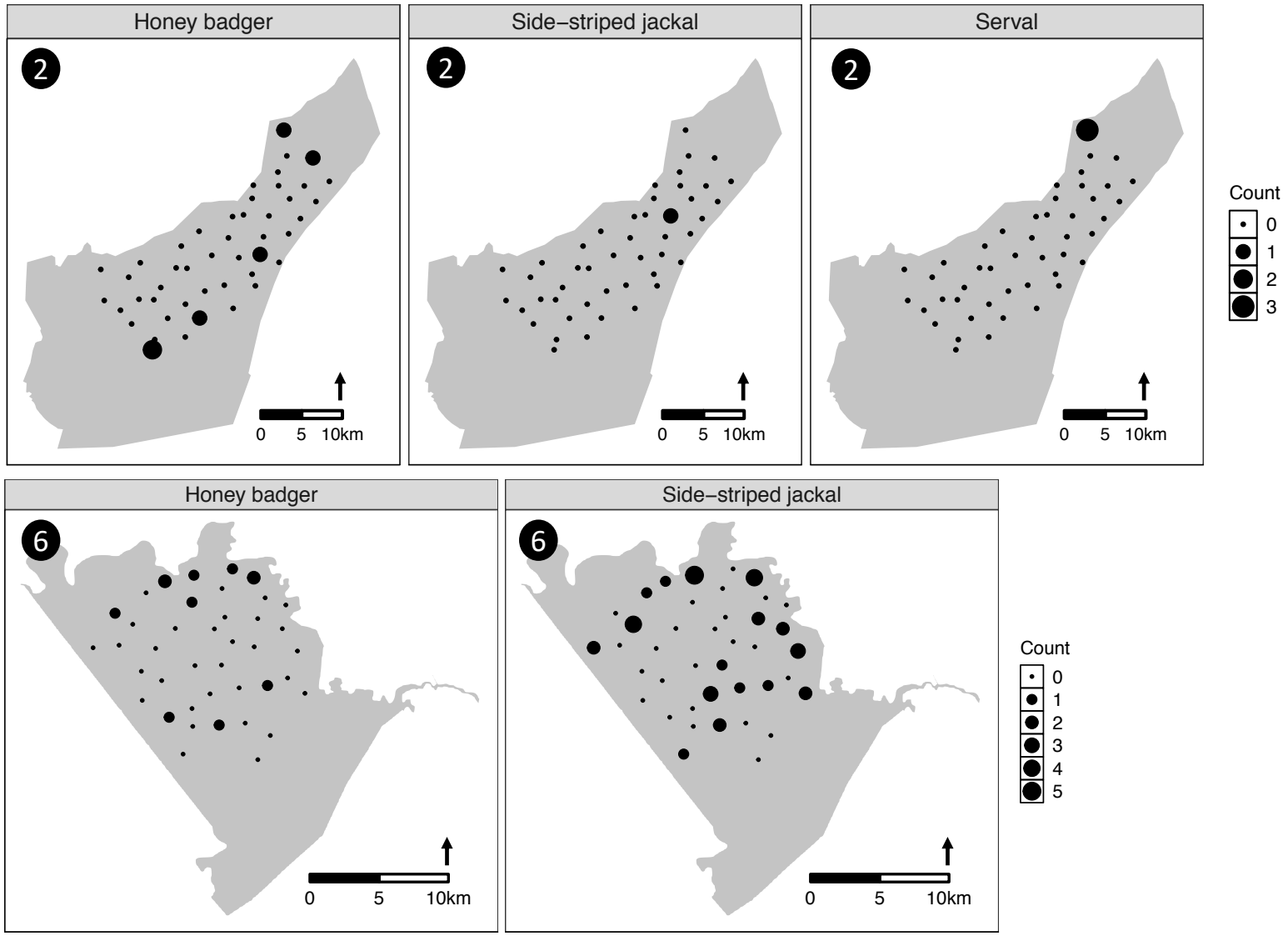

Figure 3.3 Mesocarnivore capture frequencies recorded at camera trap stations in 2) Hluhluwe-Imfolozi Park (HiP) and 6) uMkhuze Game Reserve during 2015 surveys. Numbers correspond to survey number in Figure 2.1. Points represent station locations scaled by the number of independent captures (counts) of that species.

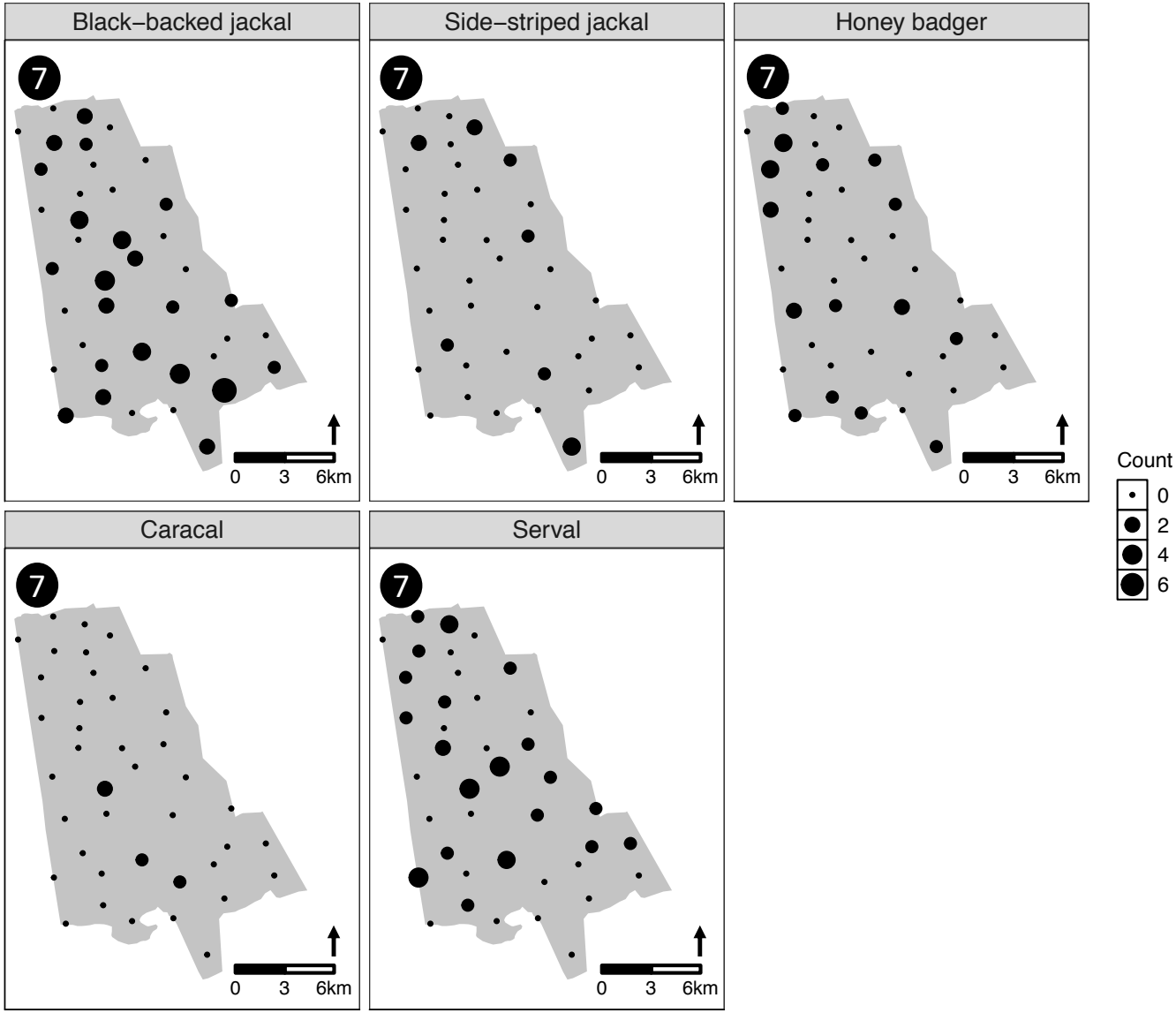

Figure 3.4 Mesocarnivore capture frequencies recorded at camera trap stations in 7) Zululand Rhino Reserve (ZRR) during 2015 surveys. Numbers correspond to survey number in Figure 2.1. Points represent station locations scaled by the number of independent captures (counts) of that species.

3.2 | Model selection

Seven hypothesis driven candidate models were considered (Table 3.3). These models included two competition models which incorporated species interaction covariates, an anthropogenic model incorporating human disturbance, an environmental model incorporating habitat variables, two global models and a null model. Detection covariates, PA and trail, remained the same for all candidate models; thus, differences in model fit were due to occupancy covariates. Goodness of fit tests showed that model Global B, which included all of the predictor variables and leopard abundance, provided the best fit for the observed data, with the Bayesian p-value closest to 0.5 (p = 0.628) and a lack of fit statistic closest to 1 (lack of fit = 1.060; Table 3.3). All RN models had a mean $\hat{R}$ below 1.1, showing that even the model with the least fit, i.e., the lowest ranked model "Competition A", still had acceptable convergence.

Table 3.3 Summary of Royle-Nichol (RN) multi-species models ordered by decreasing model fit based on each model's Bayesian p-value, lack of fit statistic and mean Gelman-Rubin statistic ($\hat{R}$). Model covariates included NDVI (Normalized Difference Vegetation Index), TRI (Terrain Ruggedness Index), Dist2edge (distance to the edge of the PA), Dogs (domestic dog relative abundance), Leopards (leopard relative abundance), PA (survey site), and trail (feature along which the camera was placed).

Models		Bayesian p-value	Lack of fit	Mean $\hat{R}$
Global B	ψ(NDVI+TRI+Dist2edge+Dogs+Leopards+PA) p(PA+Trail)	0.628	1.060	1.020
Global A	ψ(NDVI+TRI+Dist2edge+Dogs+Apex+PA) p(PA+Trail)	0.637	1.067	1.017
Anthropogenic	ψ(Dist2edge+Dogs+PA) p(PA+Trail)	0.644	1.070	1.021
Competition B	ψ(Dogs+Leopards+PA) p(PA+Trail)	0.681	1.088	1.009
Null	ψ(PA) p(PA+Trail)	0.684	1.086	1.013
Environmental	ψ(NDVI+TRI+PA) p(PA+Trail)	0.686	1.077	1.011
Competition A	ψ(Dogs+Apex+PA) p(PA+Trail)	0.717	1.098	1.012

3.3 | Mesocarnivore detections and habitat use

There was limited variation in detection probability of the five species across the PAs (Figure 3.5), with most probabilities falling below 0.1. The highest detection probabilities were obtained for black-backed jackals in Somkhanda and serval in HiP (Figure 3.5) with detection

for both species localized to small regions of each PA (Figure 3.2 and 3.3 respectively). This translated to lowered probabilities of habitat use for serval and black-backed jackal in both PAs (Figure 3.5). Habitat use varied more between species and PAs than detection probability, with 30% of the mesocarnivore species having a probability of use greater than 0.5 (Figure 3.5). The majority of mesocarnivore species in Tembe had low estimated habitat use (< 0.03). ZRR, on the other hand, had relatively high habitat use estimates for all five detected species, with caracal and side-striped jackal greater than 0.3 and the others all above 0.65. Honey badger and serval had the highest number of detections across the PAs, which translated to a higher probability of habitat use (Figure 3.6). Black-backed jackals had the highest probability of detection. Though it is important to note that there were no significant differences in detection or probability of habitat use between species (Figure 3.6). The likelihood of a mesocarnivore species being present, but overlooked by the camera survey, was generally low ($w \approx 0.2$, Table 3.4), with the highest probability for side-striped jackals in Ithala ($w = 0.4$).

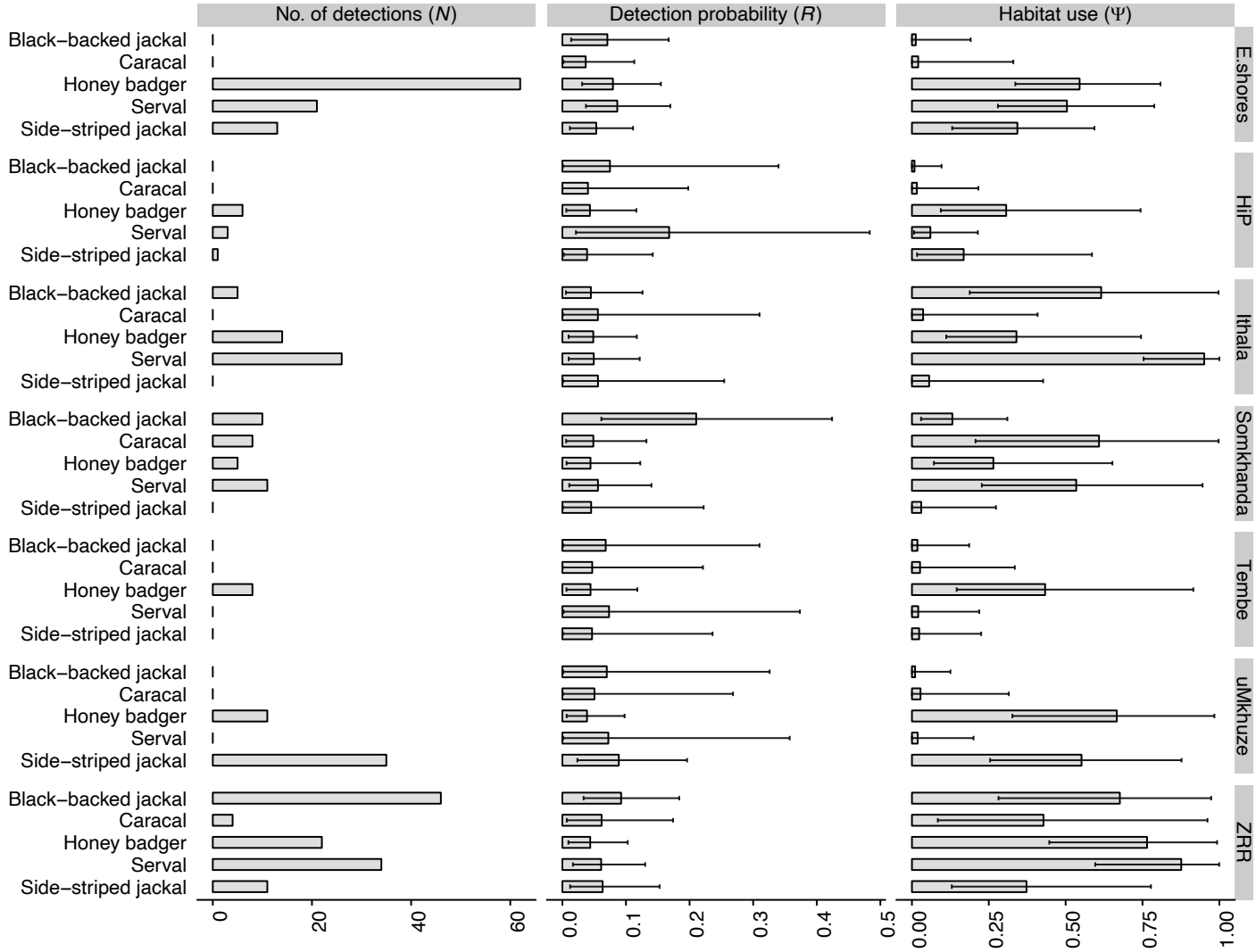

Figure 3.5 Species-specific detection and habitat use estimates per PA. Distribution of the total number of detections for 5-day pooled data (*N*), mean per-individual detection probabilities (*R*) and mean use (ψ). PAs included Eastern Shores Section of iSimangaliso Wetland Park (E.shores), Hluhluwe-Imfolozi Park (HiP), Ithala Game Reserve, Somkhanda Game Reserve, Tembe Elephant Park, uMkhuze Game Reserve and Zululand Rhino Reserve (ZRR). Error bars show 95% Bayesian credible intervals.

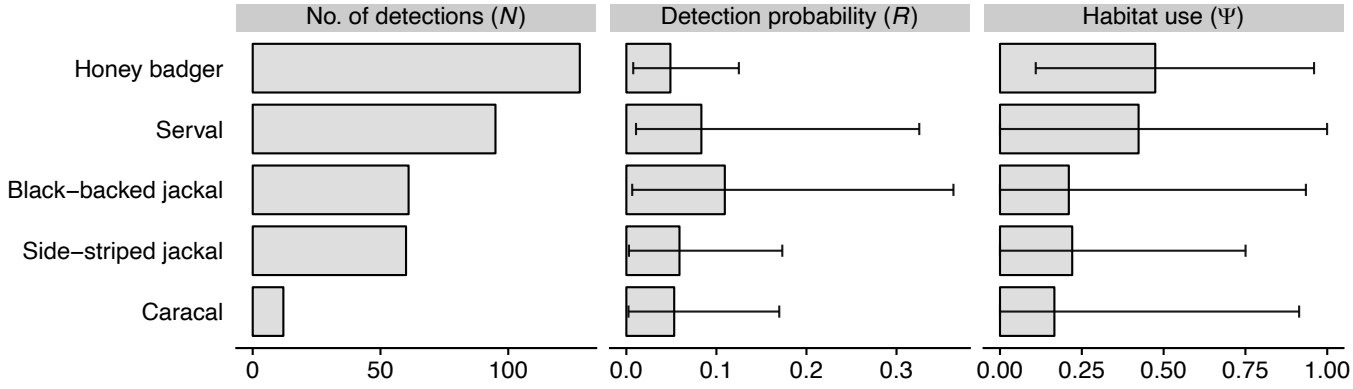

Figure 3.6 Species-specific detection and habitat use estimates across all PAs. Distribution of the total number of detections for 5-day pooled data (*N*), mean per-species detection probabilities (*R*) and mean use (ψ) across all seven PAs in KZN, namely Eastern Shores Section of iSimangaliso Wetland Park (E.shores), Hluhluwe-Imfolozi Park (HiP), Ithala Game Reserve, Somkhanda Game Reserve, Tembe Elephant Park, uMkhuze Game Reserve and Zululand Rhino Reserve (ZRR). Error bars show 95% Bayesian credible intervals.

Table 3.4 Probability of presence (w) for each mesocarnivore species for each PA in KZN. w = 1.000 indicates that the species was detected by the camera survey, w < 1.00 is the probability of the species being present but overlooked by the camera survey.

Species	Eastern Shores	HiP	Ithala	Somkhanda	Tembe	uMkhuze	ZRR
Black-backed jackal	0.079	0.117	1.000	1.000	0.172	0.137	1.000
Caracal	0.084	0.135	0.212	1.000	0.173	0.193	1.000
Honey badger	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Serval	1.000	1.000	1.000	1.000	0.202	0.186	1.000
Side-striped jackal	1.000	1.000	0.395	0.287	0.245	1.000	1.000

None of the modelled covariates had a significant effect on community-level (Figure 3.7) or species-level habitat use (Figure 3.8; BCI overlap zero). TRI, leopard abundance and domestic dog abundance all had a negative effect on mesocarnivore habitat use and had the narrowest BCIs (Figure 3.7), whilst NDVI and distance to edge had a positive influence on mesocarnivore use of PAs.

Species-level response to the different covariates varied markedly (Figure 3.8). Serval and caracal habitat use were positively associated with distance to PA edge. Serval and side-striped jackal habitat use increased with higher domestic dog abundance. Honey badger had

the largest positive association with leopard abundance, whilst black-backed jackals had the largest negative association with leopard abundance.

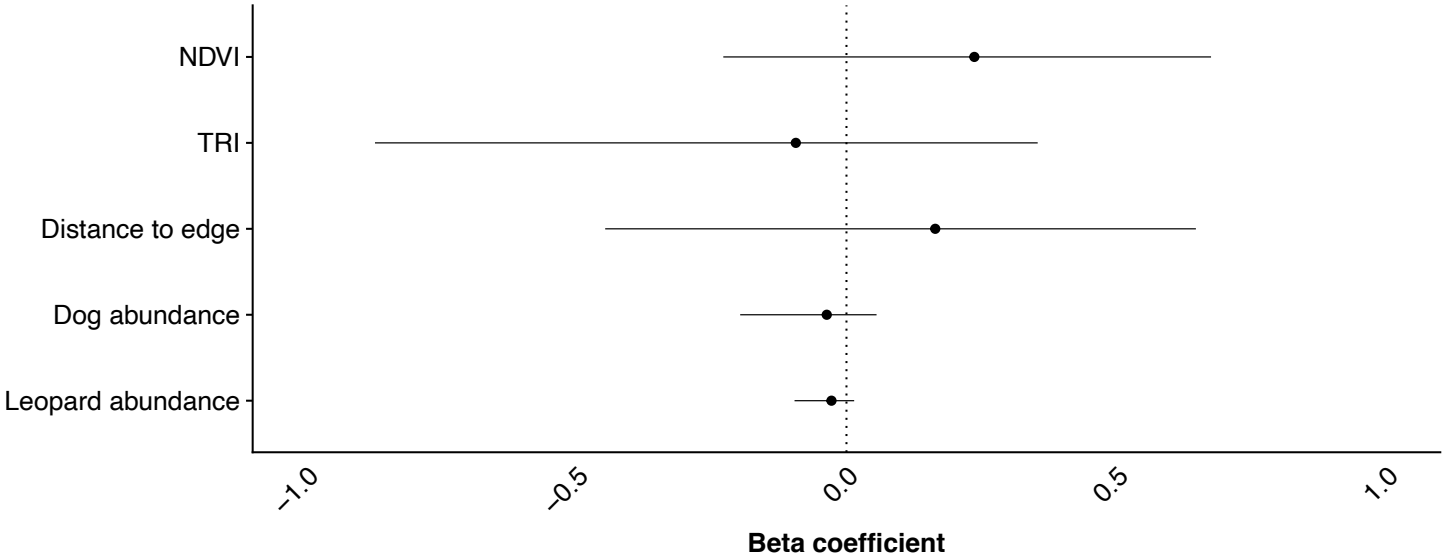

Figure 3.7 Influence of standardized hyperparameters on community-level mesocarnivore habitat use of PAs in KZN, based on the RN model. Hyperparameters included NDVI (Normalized Difference Vegetation Index), TRI (Terrain Ruggedness Index), Distance to the edge of the PA, Dog abundance (Domestic dog relative abundance), and Leopard relative abundance. Points indicate the posterior mean, and lines give the 95% Bayesian credible intervals. PA was also included as a habitat use hyperparameter but BCI range was exceedingly large (-18.885 to 17.890), and thus was not included in this graph. Additionally, detection hyperparameters Trail (feature along which the camera was placed) and PA (survey site) were tested but BCI ranges were also exceedingly large (-18.701 to 17.925 and -18.885 to 17.890 respectively), and thus were not included in this graph.

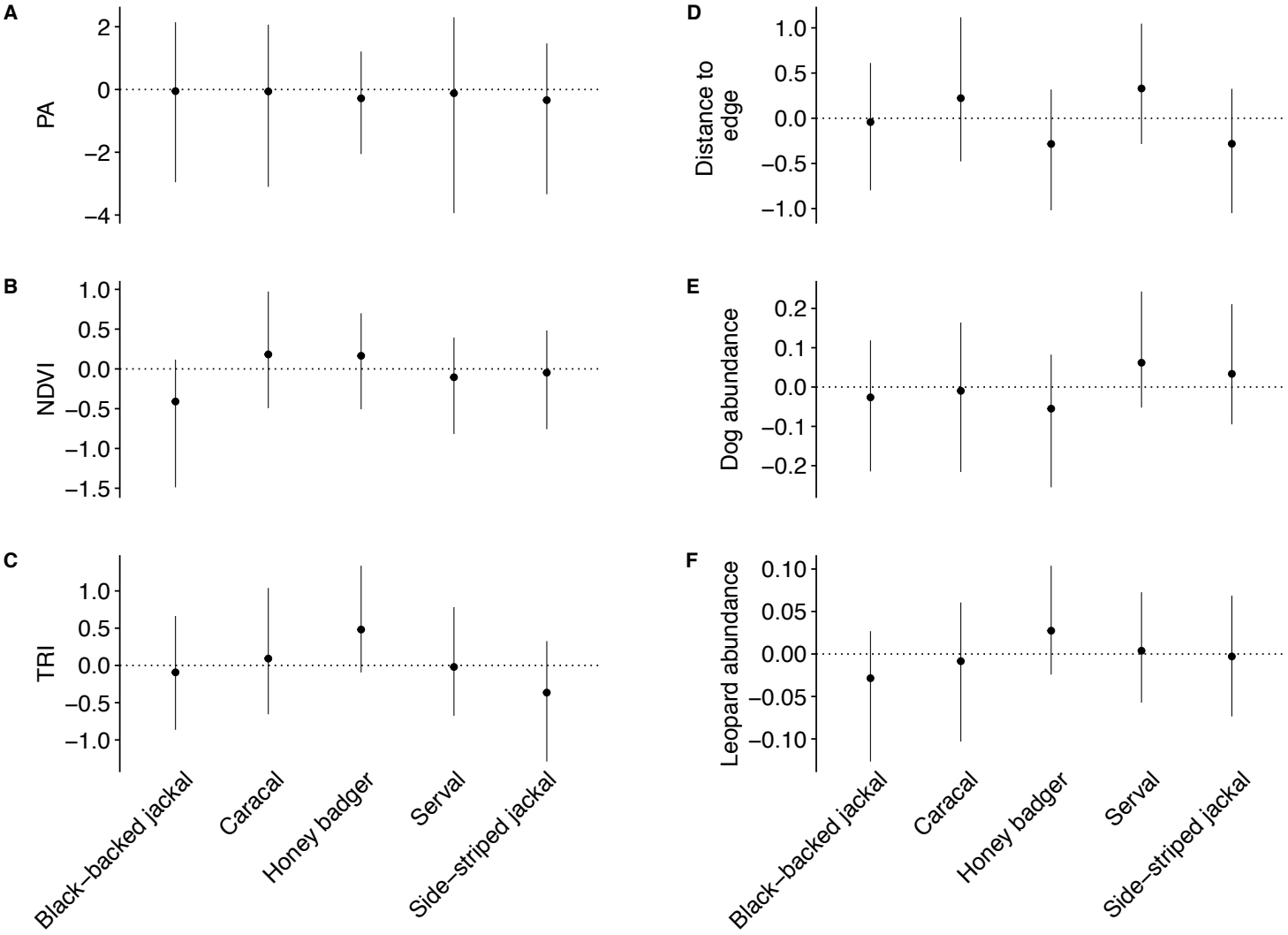

Figure 3.8 Influence of covariates on species-specific habitat use. Standardized beta coefficients and 95% Bayesian credible intervals for the influence of A) Protected Area (PA), B) Normalized Difference Vegetation Index (NDVI), C) Terrain Ruggedness Index (TRI), D) Distance to the edge of the PA, E) Domestic dog relative abundance and F) Leopard relative abundance on mesocarnivore species use of the area around the camera stations across PAs in KZN, based on the RN model. Note different scales of y-axes (A-F).

3.4 | PA mesocarnivore species richness

Overall, mesocarnivore species richness varied between the different PAs (Figure 3.9). The highest species richness was estimated for ZRR, where all five (100%) mesocarnivore species were detected (Figure 3.9), while Tembe had the lowest species richness with a mean species richness of 1.79 (36%). This pattern was also seen in the total number of species recorded (Table 3.1), with ZRR having the highest number of species (48), and Tembe having the lowest (40). Across all the PAs, the mean estimated species richness was higher than the total

number of detected species (Figure 3.9), revealing that the model took into account individual species detection probabilities. Somkhanda had a significantly higher estimated species richness compared to that of Eastern Shores, HiP, Tembe and uMkhuze (no BCI overlap). Tembe had a significantly lower estimated species richness relative to HiP, Ithala, Somkhanda, and ZRR. Species richness estimates were less precise, that is exhibited greater standard deviations and wider BCIs, for surveys with lower survey effort, i.e., Tembe and Ithala (Table 2.1).

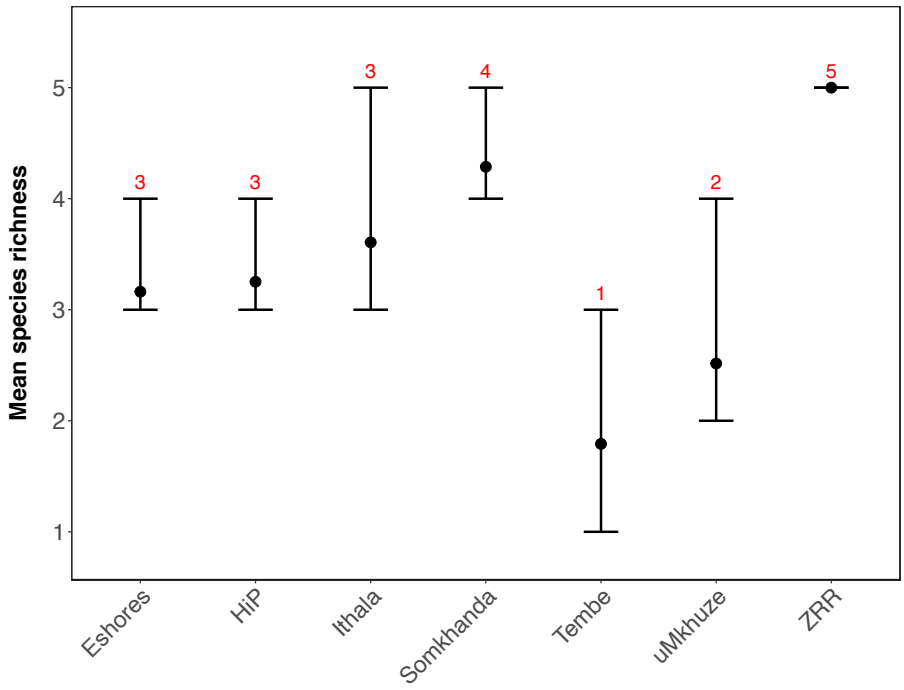

Figure 3.9 Estimated PA-level mesocarnivore species richness. Points represent estimated mean species richness and error bars represent 95% Bayesian credible intervals around estimated means. Red numbers represent the total number of detected mesocarnivore species within that PA.

3.5 | Covariates influencing mesocarnivore species richness

The best fitting GAM (Table 3.5) was Global B, which had the lowest AIC (642.53) and the highest explained deviance, accounting for 30.5% of the deviance shown in the data. NDVI, distance to the edge of the PA and leopard abundance all had statistically significant effects on mesocarnivore species richness (Figure 3.10; Table 3.5). Partial response plots showed species richness being greater at lower NDVI values, followed by a U-shaped dip in species richness for increasing NDVI (Figure 3.10). Distance to the edge of the PA had the clearest

relationship with species richness, with the estimated number of mesocarnivore species increasing closer to the boundaries of the PA. Although leopard abundance as a predictor variable provided a statistically good fit to the data, it was difficult to interpret the complex relationship with mesocarnivore species richness. TRI did not have a significant effect on mesocarnivore richness, and domestic dogs showed an extremely variable effect, with the confidence bands being too wide to make any inferences (Figure 3.10).

A different GAM was also produced for the second best-fit model (Global A, Table 3.3), but only accounted for 25.6% of the deviance shown in the data (Table 3.6). NDVI, TRI, distance to PA edge and apex predator relative abundance all had statistically significant effects on mesocarnivore species richness (Table 3.6; Figure 3.11). Relationships between species richness and NDVI, TRI and distance to PA edge showed similar associations seen in the original GAM, based on Global B (Figure 3.10). Apex predator abundance appeared to have a quadratic relationship with mesocarnivore species richness, with an initial decline followed by a gradual increase in richness with greater abundance of apex predators (Figure 3.11). Finally, variation in species richness was significantly influenced by NDVI and domestic dog abundance (Table 3.7). Both variables showed inverse relationships with species richness variance, with increased NDVI and dog abundance resulting in reduced variability in station-level mesocarnivore richness estimates, or a more homogenous richness landscape.

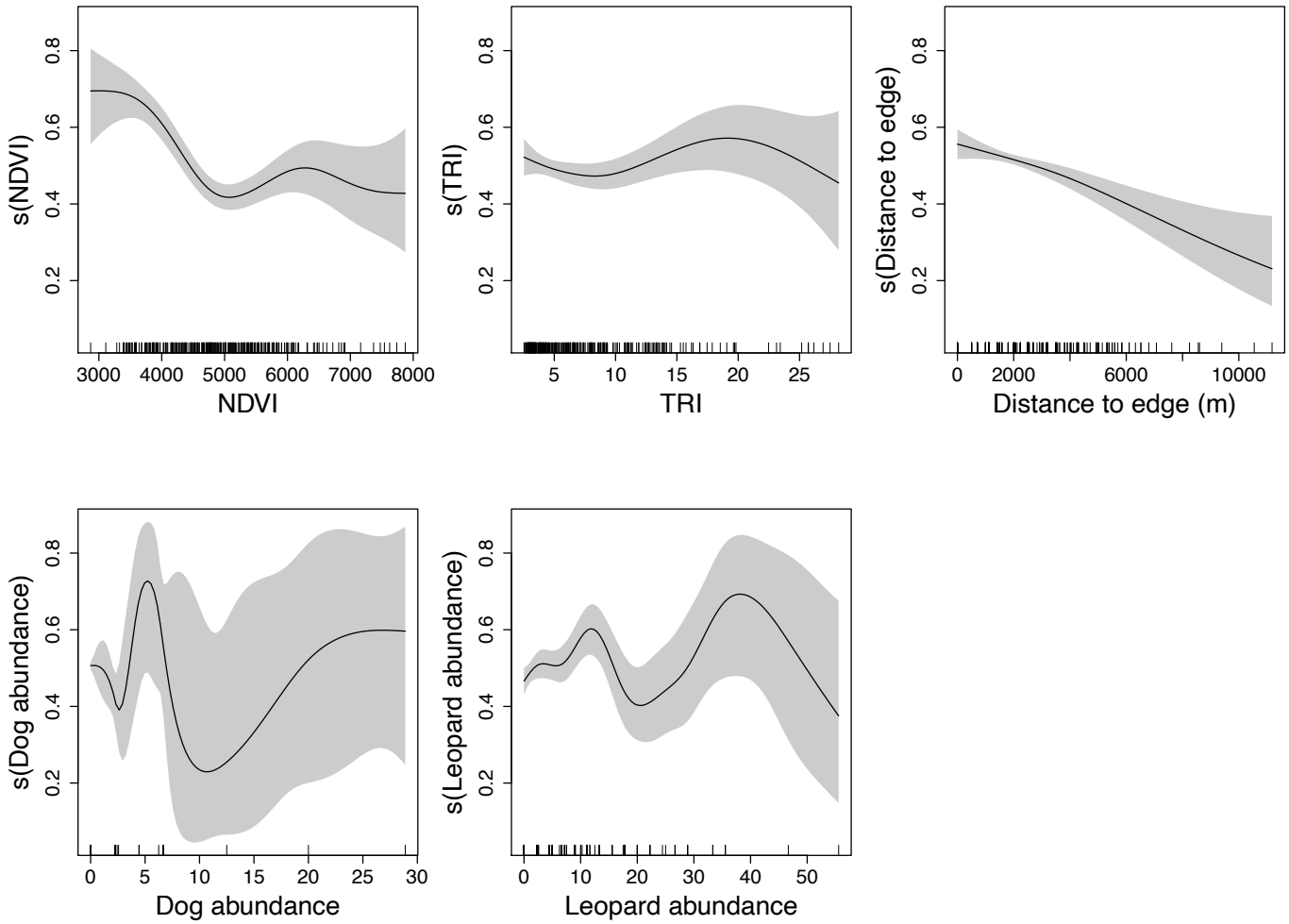

Figure 3.10 Generalised Additive Model (GAM) plots, based on Global B (Table 3.3 and Table 3.5), showing the partial effects of selected covariates on mesocarnivore species richness in PAs in KZN. The x-axis is the range of the specified covariate, with the tick marks representing locations of observed data points. The y-axis is the additive contribution of the covariate to the non-parametric GAM smoothing function. Grey shaded areas indicate the 95% confidence intervals.

Table 3.5 Estimated GAM coefficients ordered by best-fitting model based on Akaike's Information Criterion (AIC) and percentage deviance explained (Dev%). Global model based on Global B (Table 3.3). Estimated degrees of freedom (Edf), F-statistic (F), and probability level of significance (P) also provided. P-value codes: "***"P<0.001, "**"P<0.01, "*"P<0.05, and " "P>0.05. Model covariates included NDVI (Normalized Difference Vegetation Index), TRI (Terrain Ruggedness Index), Dist2edge (distance to the edge of the PA), Dogs (Domestic dog relative abundance) and Leopards (leopard relative abundance).

Model and covariates	Edf	F	P	AIC	Dev(%)
Global					
s(NDVI)	4.197	5.848	***	642.528	30.5
s(TRI)	3.129	0.572			
s(Dist2edge)	1.624	2.312	***		
s(Dogs)	5.701	1.255			
s(Leopards)	6.474	1.962	**		
Environmental					
s(NDVI)	4.198	4.344	***	668.466	15.1
s(TRI)	2.983	0.699			
Anthropogenic					
s(Dist2edge)	5.242	3.058	***	682.608	9.27
s(Dogs)	4.464e-10	0.000			
Competition					
s(Dogs)	5.016e-09	0.000		696.903	5.26
s(Leopards)	6.547	1.345			

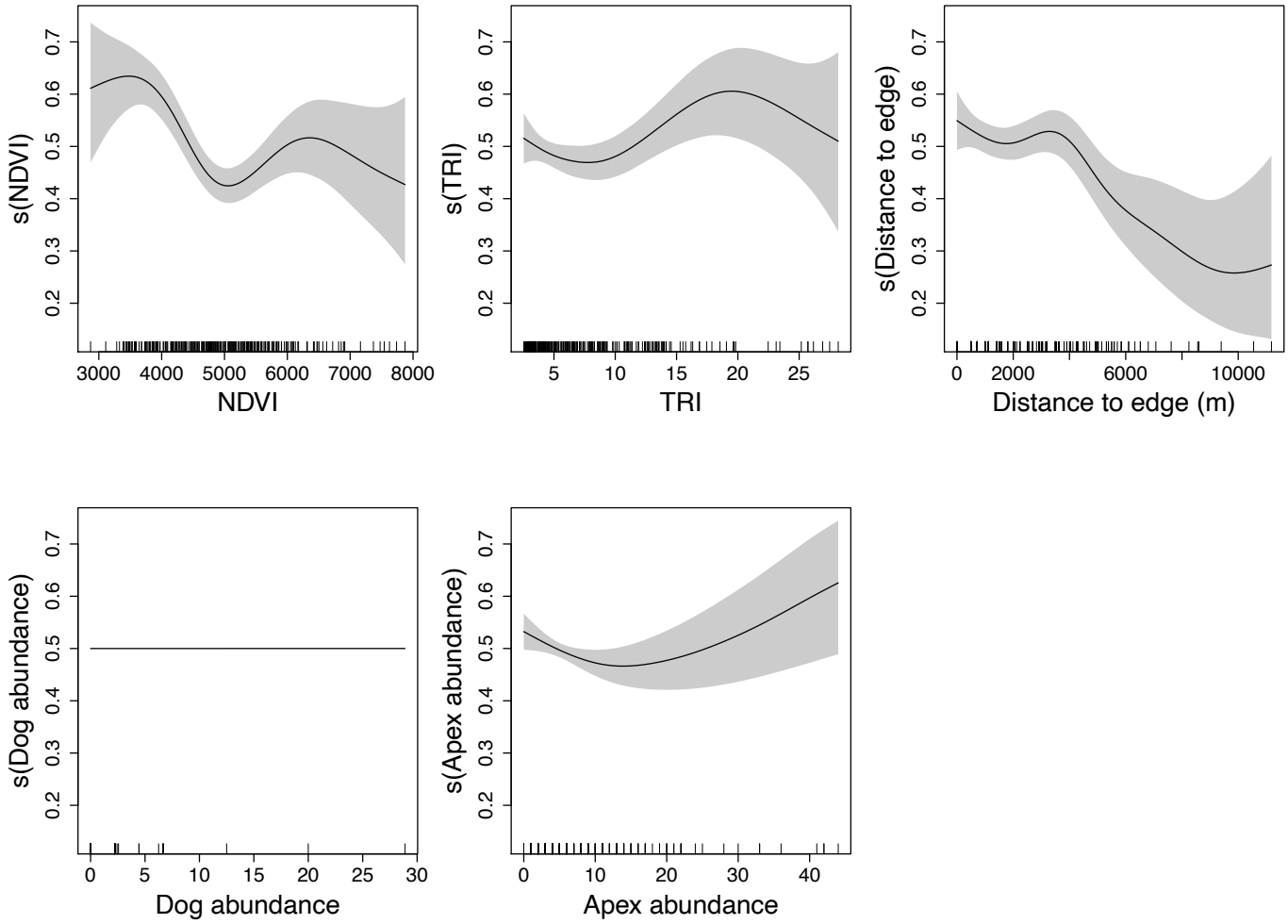

Figure 3.11 Generalised Additive Model (GAM) plots, based on Global A (Table 3.3 and Table 3.5), showing the partial effects of selected covariates on mesocarnivore species richness in PAs in KZN. The x-axis is the range of the specified covariate, with the tick marks representing locations of observed data points. The y-axis is the additive contribution of the covariate to the non-parametric GAM smoothing function. Grey shaded areas indicate the 95% confidence intervals.

Table 3.6 Estimated GAM coefficients based on Global A (Table 3.3). Estimated degrees of freedom (Edf), F-statistic (F), probability level of significance (P), and percentage deviance explained (Dev%) all provided. P-value codes: "***"P<0.001, "**"P<0.01, "*"P<0.05, and " "P>0.05. Model covariates included NDVI (Normalized Difference Vegetation Index), TRI (Terrain Ruggedness Index), Dist2edge (distance to the edge of the PA), Dogs (Domestic dog relative abundance) and Apex (apex predator relative abundance).

Model and covariates	Edf	F	P	Dev(%)
Global				
s(NDVI)	4.258	3.896	***	25.6
s(TRI)	3.329	0.902	*	
s(Dist2edge)	4.184	2.491	***	
s(Dogs)	6.177e-07	0.000		
s(Apex)	1.796	0.037	*	

Table 3.7 Mean estimates, standard deviation and 95% Bayesian credible intervals of the covariates hypothesized to influence the variance in station-specific (point-level) species richness. Values in bold indicate covariates for which the credible intervals (95% BCI) did not overlap zero. Model covariates included NDVI (Normalized Difference Vegetation Index), TRI (Terrain Ruggedness Index), Dist2edge (distance to the edge of the PA), Dogs (domestic dog relative abundance), and Leopards (leopard relative abundance). Mean Gelman-Rubin statistic ($\hat{R}$) also reported and showed convergence for all covariates.

Parameters		Mean	Standard deviation	95% BCI		$\hat{R}$
γ_0	Mean richness	-0.238	0.135	-0.498	0.028	1.00
χ_0	Mean variance	1.317	0.058	1.278	1.429	1.00
$\boldsymbol{\chi_1}$	**NDVI**	**-0.335**	**0.091**	**-0.399**	**-0.150**	**1.00**
χ_2	TRI	-0.166	0.108	-0.372	0.048	1.00
χ_3	Dist2edge	-0.011	0.103	-0.206	0.196	1.00
$\boldsymbol{\chi_4}$	**Dogs**	**-0.082**	**0.034**	**-0.138**	**-0.008**	**1.00**
χ_5	Leopards	-0.020	0.013	-0.046	-0.007	1.00

4 | DISCUSSION

Mesocarnivores persist across diverse human-modified ecosystems including agricultural (Drouilly, Clark and O'Riain, 2018), peri-urban (Serieys *et al.*, 2019), industrial (Loock *et al.*, 2018) and protected (Tambling *et al.*, 2018) landscapes. Given the extent of human-wildlife conflict in agricultural and peri-urban areas, PAs are often presumed to provide an essential refuge for wildlife including mesocarnivores. Yet this may not be the case, as PAs face a wide variety of threats and include a range of management practices that can reduce their conservation potential (Balme, Slotow and Hunter, 2010; Watson *et al.*, 2014; Santini *et al.*, 2016) and even actively persecute mesocarnivores such as black-backed jackal (Nattrass and Conradie, 2015; Minnie, Gaylard and Kerley, 2016). My study investigated mesocarnivore habitat use and species richness across seven PAs in KZN, South Africa, and revealed that not only was habitat use low for most species, but many were not detected in multiple PAs. In addition, my results support previous research showing that the composition of mesocarnivore communities within PAs are shaped by interacting factors such as habitat requirements, interspecific relationships and intermediate levels of disturbance.

4.1 | Detections

My study revealed a surprisingly low number of detections (N = 356) for all five mesocarnivore species (black-backed jackal, caracal, honey badger, serval and side-striped jackal), across the surveyed PAs. Mesocarnivores in PAs have been shown to outnumber larger predators by as much as 9:1 (Carbone and Gittleman, 2002; Roemer, Gompper and Van Valkenburgh, 2009). For instance, in a study by Kok (2015), black-backed jackal detections (N > 1000) vastly outnumbered both leopard (N = 27) and lion (N = 4) in PAs in the Fish-Kowie corridor, Eastern Cape. However, this was not the case for my study where detections of leopards (N = 1060), lions (N = 488) and spotted hyaena (N = 985) far exceeded those of the most detected mesocarnivore species, honey badger (N = 128). Low detections of mesocarnivores have limited previous studies in KZN (Ehlers Smith, 2016), where activity patterns of black-backed jackals could only be calculated in farmlands, as the number of detections within PAs were too low (N < 50) to compute the required statistics.

Detections of mesocarnivores varied markedly across my surveyed PA network. Tembe had the lowest number of detections across all focal species with honey badger being the only mesocarnivore detected (N = 8; Table 3.2). HiP had the second lowest total number of mesocarnivore detections (N = 10), however these were spread over three species, namely honey badger, side-striped jackal and serval.

Similarly low detections of honey badger, side-striped jackal and serval have been reported in Maputaland Conservation Unit (Ramesh *et al.* 2016) and of black-backed jackal in Anysberg Nature Reserve (Drouilly, Clark and O'Riain, 2018). Both studies surveyed for total mammalian species richness and occupancy using a systematic random camera trapping design (see Figure 1.1). This camera station arrangement is more suited to multi-species analyses, compared to my targeted probabilistic survey design, as camera placement is not biased towards the detection of a single species (Harmsen *et al.*, 2010). As camera station feature had no significant effect on species detection in my surveys and the results conformed with studies that utilized different methodologies, the low detection of mesocarnivores in my study is likely to be a true reflection of their rarity in the areas sampled, despite the detection biases inherent in my survey design (Gu and Swihart, 2004). Inferences for rare species will always be hampered by small sample sizes (Tobler *et al.*, 2008) and indeed habitat use estimates and parameter beta coefficients were more precise for species with a greater number of detections (i.e., honey badgers; Figure 3.6 and 3.8). However, it is important to note that, despite the low detections of mesocarnivore species, the model fitted my data well ($\hat{R}$ = 1.02; Table 3.3) and the fact that mesocarnivore detections were so low is in itself very interesting and warrants further study.

4.2 | Mesocarnivore species richness patterns and species-specific responses

The relationship between mesocarnivore species richness and the selected covariates were explored using GAMs. Species richness estimated for each camera station was found to decline with increased vegetation and leopard abundance, and increase closer to the edges of the PAs. Suggesting (1) the edges may provide a refuge for mesocarnivores from more dominant species, (2) the edges may be more inviting due to increased carrying capacity and (3) mesocarnivores exhibit resilience/adaptability to intermediate human disturbance at PA

edges. The variation in species richness between stations showed that species richness variance decreased significantly (BCI did not overlap zero) with NDVI and domestic dog abundance. This suggests that primary productivity and domestic dog abundance modify mesocarnivore distributions through a PA, potentially offsetting the benefits of the edge zones for select species.

Intensive anthropogenic land-use surrounding PAs can create edge effects, whereby the peripheries of PAs experience elevated levels of degradation relative to their cores (Woodroffe and Ginsberg, 1998; Massey, King and Foufopoulos, 2014). PA perimeter fence lines are often cleared of native vegetation for management purposes such as security patrolling, firebreaks, or reducing arthropod disease vectors such as brown ear tick *Rhipicephalus appendiculatus* (Lindsey *et al.*, 2011; Somers and Hayward, 2012). This land transformation may facilitate colonisation by invasive plant and animals species (Hobbs and Huenneke, 1992; Kolar and Lodge, 2001), especially when adjacent to farmland. Mesocarnivores have been shown to take advantage of the trophic resource enhancement created by agrosystems, which can increase the overall carrying capacity of a landscape (Verdade *et al.*, 2011; Williams *et al.*, 2017). For example, caracals have been found to spend a sizeable amount of time foraging in vineyards in Cape Town (Serieys *et al.*, 2019), and their rapid range expansion in KZN has been attributed to their ability to take advantage of resource enhancement by farming practices in agri-ecosystems (Ramesh, Kalle and Downs, 2017a). Additionally, within KZN, estimated occurrences of honey badgers were greater in human-modified landscapes than natural vegetation types (Kheswa *et al.*, 2018). Edges are a good proxy for areas of intermediate disturbance with the latter often associated with higher levels of species diversity (Knight and Landres, 2002), which is consistent with the findings of my study.

Research has shown that reserve edges form population sinks for large predators (Loveridge *et al.*, 2010; Massey, King and Foufopoulos, 2014), resulting in reduced use of peripheral areas (Kiffner, Stoner and Caro, 2013). For example, illegal killing and poaching caused reductions in the density of lions in the peripheral areas of the Serengeti National Park, Tanzania, in the 1990s (Packer, Scheel and Pusey, 1990). Edge effects have also been shown to have negative behavioural effects on spotted hyaenas in the Masai Mara National Reserve, Kenya (Pangle

and Holekamp, 2010), and have been suggested as ecological traps for other large carnivores, such as leopards (Balme, Slotow and Hunter, 2010). Conversely, mesocarnivores may not be as susceptible to poaching methods, such as snares, along PA edges. For instance, both black-backed jackals and caracals have been shown to be incredibly trap shy (Bothma, 2012) and will rarely, if ever, be trapped a second time (Hey, 1964). As a result, mesocarnivores may not experience these negative edge effects to the same degree as larger carnivores. This trap-shyness could also account for the low detection probabilities across the mesocarnivore species studied.

Apex predators often shift mesocarnivores from optimal localities (Creel, 2001; Vanak *et al.*, 2013; Swanson *et al.*, 2014). This has been shown in the USA where coyotes (*Canis latrans*) actively displaced San Joaquin kit foxes (*Vulpes macrotis mutica*) from the best foraging habitats to more marginal habitat (Nelson *et al.*, 2007). Therefore, edges may in fact provide a safer niche for mesocarnivores within PAs with larger predators. Black-backed jackal occupancy has been found to be significantly higher in the absence of apex predators, with distributions more concentrated where apex predator activity is lower, suggesting spatial avoidance (Taylor, 2015). The displacement of mesopredators by larger carnivores, such as leopards, is consistent with the "landscape of fear" theory (Brown, Laundré and Gurung, 1999), which has been shown to apply to predators in African savannahs (Riginos and Grace, 2008) and is consistent with my findings of higher mesocarnivore species richness in the more human-impacted edges of PAs.

Although I found mesocarnivore species richness to be generally inversely related to leopard abundance (Figure 3.10) this relationship was non-linear and suggests the effects of multiple interacting variables, some of which were not evaluated in my study. It has been noted that more diverse predator guilds exert weaker, more diffuse top-down control than less diverse predator guilds (Elmhagen *et al.*, 2010). The GAM incorporating all three apex predators (leopards, lions and spotted hyaena; Figure 3.11), showed a different relationship with mesocarnivore species richness than leopard abundance alone (Figure 3.10). Initial increases in apex predator abundance resulted in a reduction in mesocarnivore species richness, in accordance with the leopard GAM and mesopredator suppression theory (Prugh *et al.*, 2009). However, at greater apex predator abundance, mesocarnivore species richness increased.

This may be accredited to food provisioning through increased scavenging opportunities from lions and spotted hyaena. In ungulate birthing periods, black-backed jackals have been found to feed almost exclusively on calves (Klare *et al.*, 2010). This could lead to short-term dietary overlap with larger carnivores, and thus increased competition. Outside of these periods, foraging on carrion provided by larger carnivores could reduce competition and allow mesocarnivore species richness to increase. This has previously been seen in the Karoo National Park, where black-backed jackals initially took advantage of abundant springbok (*Antidorcas marsupialis*) populations, however subsequent to lion reintroductions, switched to foraging more on carrion (Fourie *et al.*, 2015). Future studies should explore interspecific and spatial dependence between mesocarnivores and larger predators in PAs, and how this relationship may change due to seasonal food demands.

When primary productivity is high, top-down effects exert a greater impact on mesocarnivore population regulation (Elmhagen and Rushton, 2007; Prugh *et al.*, 2009; Pasanen-Mortensen, Pyykönen and Elmhagen, 2013). Kok (2015) and Drouilly, Clark and O'Riain (2018) both found higher black-backed jackal and caracal occupancy in areas with lower net primary productivity. This relationship also appeared in my results with mesocarnivore species richness being inversely related to NDVI (Figure 3.10). Variation in species richness estimates across PAs were also significantly explained by NDVI (Table 3.7). This relationship is further supported by the GAM incorporating apex predators (and greater variability) still producing a similar association between species richness and NDVI (Figure 3.11).

Mesocarnivore abundance has been shown to vary depending on individual species sensitivity to fragmentation and anthropogenic factors (Baker and Leberg, 2018). Although species richness increased towards the peripheries of the PAs, mesocarnivore species were not absent from the core regions (Figure 3.1 to 3.4). Serval have been shown to prefer wetlands with natural vegetation, especially in fragmented and transformed landscapes (Ramesh and Downs, 2015a). Whilst the relationship was not significant (BCI overlapped zero), servals in my study showed a positive association between habitat use and distance to PA edge, suggesting a preference for the less human-disturbed core areas (Figure 3.8). Honey badgers were the most detected mesocarnivore species in my study and had the highest probability of using PAs (ψ = 0.47; Figure 3.6). Generally occurring at low densities, honey badgers are

particularly sensitive to human-wildlife conflict as they are threatened by indirect persecution methods aimed at jackal species and caracal (Do Linh San *et al.*, 2016). My results showed a positive, though not significant, association between honey badger habitat use and leopard abundance (Figure 3.8), suggesting that honey badger are less susceptible to pressures imposed by larger predators than other mesocarnivore species (Estes, 1992; Begg, 2002). This relationship may have contributed to the positive association observed in the apex predator GAM (Figure 3.11), where mesocarnivore species richness increased with greater apex predator abundance. These findings agree with a study conducted in the Serengeti National Park, Tanzania, where honey badger distributions were positively associated with the relative abundance of lion and spotted hyaena (Allen, Peterson and Krofel, 2018). This lack of predator exclusion may allow honey badgers to seek refuge within PAs, away from human conflict. Caracal and black-backed jackals, on the other hand, are strongly associated with peri-urban and agricultural areas where they readily exploit small livestock (Perrin, 2002; Drouilly *et al.*, 2018) and despite sustained persecution are currently expanding their distribution and livestock impacts in the Karoo (Drouilly *et al.*, 2018). In my study, caracal and the two jackal species had comparatively lower probabilities of using PAs than serval and honey badgers (Figure 3.6). It is possible that these species do better outside of PAs where they encounter abundant food in the form of livestock and experience less competition from other predators including larger species (Humphries *et al.*, 2016). Within PAs they may exploit the smaller peripheral zones which are closer to livestock farms and in so doing drive the observed trend of increased mesocarnivore species richness towards the PA edges.

Domestic dog disturbance in the peripheries of PAs is a global problem and has been reported across continents such as Asia (Home, Bhatnagar and Vanak, 2018), South America (Lacerda, Tomas and Marinho-Filho, 2009), North America (Reed and Merenlender, 2011) and Africa (Newmark, 2008). In my study, domestic dogs were found to significantly influence the pattern of mesocarnivore species richness in PAs, by decreasing variation and smoothing species richness estimates across the landscape (Table 3.7). The presence of domestic dogs within a PA could suggest a certain amount of fence permeability, allowing mesopredators to move across PA boundaries. Additionally, wildlife poachers frequently use domestic dogs for hunting purposes, and thus their presence could suggest increased human pressure within the bounds of the PA. As domestic dogs dominate PA edge zones (Torres and Prado, 2011),

mesocarnivores have an increased chance of incidental encounters with individual dogs and hunting packs in these areas. However, domestic dog abundance should decrease further into the PA as the chance of encountering anti-poaching teams and other dangerous wildlife increases. Domestic dogs, depending on their size, can act as meso- or large carnivores, with their relative impacts likely determined by their status and roles at the time they are present within a PA and its edges. That is, if large dogs are accompanied by people as hunting aids, their impact will be different to those acting as companions or those that are unaccompanied by people (Sparkes, Ballard and Fleming, 2016; Hudson *et al.*, 2017; Gabriele-Rivet *et al.*, 2019). Further analyses should separate domestic dogs into size and accompaniment categories, if sample size permits, so analyse this possible effect.

Domestic dogs have been found to influence native species through predation (Dickman *et al.*, 2013), competition (Vanak *et al.*, 2014), disturbance (Zapata-Ríos and Branch, 2016, 2018), hybridization (Bassi *et al.*, 2017) and disease transmission (Furtado *et al.*, 2016; Sabeta *et al.*, 2018). As such, the effects of domestic dog disturbance on species richness could manifest at the individual level, with competitive displacement or disease offsetting the benefits of the edge areas for mesocarnivores (Vanak, Thaker and Gompper, 2009). This could reduce species richness along the peripheries, by removing particularly sensitive species, weakening the positive association between mesocarnivore species richness and PA boundaries, and ultimately homogenizing the richness landscape across PAs.

In 2013, community surveys in areas surrounding KZN PAs indicated that 26% of domestic dog mortality could be attributed to diseases such as canine distemper virus and canine parvovirus (Gummow, Roefs and Klerk, 2010; Flacke *et al.*, 2013). Disease transmission between domestic dogs and mesocarnivores is clearly of conservation concern. Side-striped and black-backed jackals are particularly at risk of rabies transmission from domestic dogs (Butler, Du Toit and Bingham, 2004; Hughes and Macdonald, 2013) due to their close relatedness and high dietary overlap. Additionally, sharing water sources and large carcasses can facilitate close contact between remote individuals (Zulu, Sabeta and Nel, 2009), thus promoting high rates of disease transmission. In the 1970s, black-backed jackals disappeared from HiP, possibly as a result of a disease outbreak of sarcoptic mange, canine distemper or rabies (Whateley and Brooks, 1985; Rowe-Rowe, 1992). Several reintroduction attempts were

conducted in the 1990s (Somers *et al.*, 2017), however all were unsuccessful. In 2006, 20 African wild dogs in HiP were reported dead with anecdotal evidence suggesting disease from domestic dogs as a primary factor for the packs demise (Flacke *et al.*, 2013). It is feasible that disease transmission could alone explain the low mesocarnivore numbers in many PAs in this province.

None of the selected covariates showed a significant influence on mesocarnivore community-level habitat use (Figure 3.7). This could be a manifestation of the variability in response of the community as a whole, i.e., varying sensitivities and preferences between species (Begg *et al.*, 2003). Additionally, in a hierarchical framework, estimates for rarely observed species will be naturally drawn towards the community means, also referred to as "Bayesian shrinkage" to the mean, which could explain the variability in estimates and the lack of confidence in species-level habitat use estimates (Figure 3.6).

4.3 | PA comparisons

When comparing individual PAs, the relationship between species richness and modified landscapes remained strong. ZRR and Somkhanda had significantly higher species richness estimates compared to the Eastern Shores, HiP, Tembe and uMkhuze. Somkhanda is a relatively new PA, established in 2006 from highly disturbed land and is managed using a community-level scheme, designed to incorporate subsistence farming within wildlife management land use (Musavengane and Simatele, 2016). Similarly, ZRR was formed in 2004 on land previously used for cotton and cattle farming. Both these PAs had the lowest apex predator abundance (Table A1and A2). These results are in agreement with the literature showing that mesocarnivores are more successful when large carnivores are either absent or have reduced numbers (Thorn *et al.*, 2011, 2012) and on more modified lands (Verdade *et al.*, 2011; Drouilly, Clark and O'Riain, 2018). This has also been seen in Karingani Game Reserve, where preliminary camera trap results have shown vastly reduced jackal detections (side-striped jackals = 43; black-backed jackals = 26) in the older northern section with greater leopard captures, than in the newer southern section (side-striped jackals = 81; black-backed jackals = 555; Smythe 2019, *pers. comms.,* 13 June).

Tembe, by contrast, had the lowest mesocarnivore species richness of all seven PAs ($\bar{x}$ = 1.79). Tembe is an older more established PA (declared a Game Reserve in 1983) and surrounded by relatively low impact subsistence farming (*Hyphaene coriacea* or Ilala pine; Figure 2.1; Matthews *et al.*, 2001; Ezemvelo KZN Wildlife, 2018). Additionally, Tembe had the second highest mean NDVI of all PAs considered and had a substantially higher abundance of apex predators compared to ZRR and Somkhanda (Table A1 and A2). All of these factors, namely the lack of disturbance, high primary productivity and higher abundance of potential competitors/predators, could account for the drastically low mesocarnivore species richness in Tembe.

In my study, mesocarnivore species richness did not appear to be affected by PA size. This result is incongruent with previous studies, namely Crooks (2002), which found that total mammal species richness increased with the area of a PA in KZN. In South Africa, most conservation strategies focus on maintaining and developing small PAs to conserve biodiversity (Davies-Mostert, Mills and Macdonald, 2009). My results suggest that mesocarnivores might not thrive in small, well established PAs with larger carnivores. Given large carnivores are more threatened than their smaller counterparts it seems unlikely that these findings will lead to management changes, but it does caution against attempts at repopulating established small PAs with mesocarnivores, as was attempted in HiP for black-backed jackals in the 1990s (Somers *et al.*, 2017). Small PAs with a recent history of disturbance and a low leopard abundance, by contrast, support more mesocarnivore species and at higher relative abundance. These results are important for future IUCN assessments of mesocarnivores as the assumption that they are well conserved in PAs is clearly very open to debate; hence, the future of the guild in KZN could be more dependent on marginal habitat outside of PAs.

4.4 | Limitations and recommendations

Despite the improved occupancy estimation of rare or infrequent species through MCMC simulations, habitat use estimates were still unstable when the data were sparse (Guillera-Arroita, Ridout and Morgan, 2010; Guillera-Arroita *et al.*, 2014). This made interpreting both community- and species-level responses to the different covariates difficult (Welsh,

Lindenmayer and Donnelly, 2013), as there was a large amount of uncertainty around the estimates (Figure 3.7 and 3.8). Therefore, when studying rare ($\psi \leq 0.3$) or cryptic ($p \leq 0.3$) species (Specht *et al.*, 2017), occupancy models may still lack adequate power in discerning real differences between species. Detection estimates could have been biased by my inability to model the detection effect of the population size (i.e., species local abundance), as this required *a priori* knowledge of the population, which was not available for my study, thus violating the assumption that all variation in detection is captured by the selected detection covariates. My study took place over different seasons. This could not be controlled for as the data was inherited with the imposed study design. However, it is important to note that reproductive cycles, and hence breeding-related movements, can fluctuate seasonally and thus it is possible that season could influence detection probabilities.

Despite their complexity, RN multi-species hierarchical models are often preferred over single-species models (Tobler *et al.*, 2015; Li, Bleisch and Jiang, 2018). This is especially true when dealing with multiple species or covariates, where single-species models can become overly complicated and time-consuming to compute. In addition, RN models can easily be extended to calculate species richness estimates, demonstrated in my study, that incorporate detection probability. Few studies capitalize on the powerful community-level information available from camera trap surveys (Stoner *et al.*, 2007; Schuette *et al.*, 2013; Rich *et al.*, 2016) and are instead more focused on a single target species. With the growing use of camera trapping as a monitoring tool, my study shows that one can use such data to study both rare and common species within the same statistical framework. Additionally, this model provides the possibility of estimating the occupancy probability or habitat use of an entire community, given that undetected species can be accounted for in the modelling framework. As such, I recommend expanding this framework to all of Panthera's monitoring sites in South Africa to gain a better idea of why mesocarnivores appear to be so rare in KZN and further explore possible covariates.

Although a statistically significant relationship was found between covariate partial effects and species richness, the GAM explained only 30.5% of the variation in species richness (Table 3.5), suggesting that other variables should be explored (MacKenzie *et al.*, 2006). With more data (e.g., replicates across years) it may be possible to include additional covariates to

improve the model's strength. The best-fit occupancy model only included one large carnivore, namely leopards. Although there was a statistically significant effect of leopard abundance on mesocarnivore species richness, this relationship was non-linear and difficult to interpret. There was also a high level of uncertainty surrounding the estimate (Figure 3.10). Untangling the interspecific relationship between large carnivores and mesocarnivores is notoriously difficult (Elmhagen *et al.*, 2010; Vanak *et al.*, 2013) primarily due to the complex interplay of multiple ecological drivers. Lions were present in four out of the seven PAs surveyed. Lions are known to influence mesocarnivores by providing larger and more accessible scavenging opportunities, thereby reducing food-driven interspecific competition (Yarnell *et al.*, 2013) in addition to exerting top down control through both indirect and direct interactions. This was seen in the GAM including apex predators (Figure 3.11), where an initial decline in species richness could suggest suppressive competition, but later increases in richness possibly indicating greater foraging opportunities. Distinguishing between all possible drivers of predator distribution and abundance, such as foraging, competitor/predator avoidance, finding mates and communicating with conspecifics, is a difficult process (Elmhagen *et al.*, 2010; Majolo, 2013), but clearly required to fully understand the relationship between large- and medium-sized carnivores in PAs. Constant advances in the monitoring of fine scale movement and behavioural patterns through the deployment of bespoke GPS collars with accelerometers on multiple species at the same time will offer future researchers a chance to refine their understanding of the behavioural dynamics between members of a guild and individuals of a given species.

Black-backed jackals have been shown to dominate side-striped jackals despite their smaller size. For example, a study from early 2000 showed black-backed jackals aggressively excluding side-striped jackals from their territory (Loveridge and Macdonald, 2002). My study did not incorporate interspecific competition between mesocarnivore species. Though, it was observed that the two jackal species were rarely detected within the same PA. One exception was ZRR, but detections of side-striped jackals were still much lower than black-backed jackals overall (Figure 3.5) and appeared to be spatially segregated (Figure 3.4). This may imply some level of competitive interaction, potentially exclusion, between these two closely related species, as seen in studies by Loveridge and Macdonald (2002, 2003). Future studies should

explore this relationship, as well as other possible inter-species competition, when modelling jackal species occurrence and/or habitat use.

Diets vary markedly between mesocarnivore species and include fruits, micromammals and invertebrates (Drouilly, Nattrass and O'Riain, 2018). Although my study design, aimed at detecting leopards, could adequately detect mesocarnivores species, it would be ineffective in quantifying the broad range of food items utilized by mesocarnivores. Prey abundance can be estimated by supplementing camera trap surveys with vegetation transects as well as insect and small mammal trapping methods, which could allow for increased predictive power of the RN model. As my data were collected in 2015 and aimed at monitoring large carnivores (for which fruit, insects and small mammals are not a critical diet component) these supplementary surveys were not conducted, and thus I was unable to reliably include prey as a covariate. However, prey abundance has been shown to directly influence carnivore density (Karanth *et al.*, 2004; Ramesh and Downs, 2015b); thus, future studies should seek ways in which to include prey abundance, or dependable proxies, in their models.

Previous studies have highlighted how local primary productivity and foraging availability were strong determinants of herbivore populations in African ecosystems (Grange *et al.*, 2006; Gandiwa, 2013), which in turn, are important in regulating predator occupancy. As distance to the edge of a PA was found to significantly explain mesocarnivore species richness, understanding the vegetation structure of these peripheral areas is of great importance. One possible vegetation change is through increased colonisation by invasive plant species due to fence line clearing (Hobbs and Huenneke, 1992; Kolar and Lodge, 2001), which in turn could change the overall carrying capacity of the peripheral areas. Alien vegetation spread has been shown to be strongly linked with bare ground (Beater, Garner and Witkowski, 2008); therefore, a bare soil index such as the soil-adjusted vegetation index (MSAVI; Qi *et al.*, 1994) could be used to analyze vegetation changes along PA edges. These metrics should also be paired with field-based assessments of habitat, especially in PAs with high anthropogenic effects, in order to accurately quantify habitat quality.

Distance to the edge of a PA, although a seemingly simple metric, also has associated uncertainty as it is subject to variations in population density and land use around the PA. For

example, the type of edge or boundary may play a vital role in determining mesocarnivore habitat use within PAs. Ithala, uMkhuze and Eastern Shores have rivers serving as boundaries on one side (Figure 2.1), and therefore, could have different effects to fence line edges. Unfortunately, I did not have detailed information on the status of the boundary fences in my surveyed PAs, and thus did not include this metric in my analyses. Future studies should explore the effects of boundary type and state (i.e., holes) as this could influence net movement of mesocarnivores into and out of PAs.

Finally, Ordeñana *et al.* (2010) showed that total species richness was more affected by urban intensity not proximity to their study area. Quantifying urban intensity around the PA may be a stronger predictor of species-level effects. Additionally, the type of neighbouring land-use could also have an effect. Although livestock farms may provide greater food availability through livestock calves, sheep and goats, these areas are often associated with increased mesocarnivore persecution. Additionally, intense agricultural practices, such as cropland or permanent pastures, have been found to diminish shelter and prey availability of carnivores, ultimately resulting in highly imbalanced diets (Remonti, Balestrieri and Prigioni, 2011). Pesticides are often used on crop lands to control rodent populations and can be problematic for mesocarnivore species utilizing these areas. For example, abundance of jackal species and serval have been shown to be dramatically reduced on lands where pesticides were used (Ramesh and Downs, 2015b), and caracals utilizing vineyards in Cape Town are being found with increased concentrations of rat poisons in their livers (Serieys *et al.*, 2019). Therefore, future studies should not only look at distance to disturbance but also type, extent and intensity of land use.

4.5 | Conclusions

My study showed that camera trap data derived from a single-species survey can be used in a multi-species hierarchical modelling framework to great success, building on larger research projects as well as adding to the current knowledge on mesocarnivore community habitat use and richness in South African PAs. This result is important for PAs that experience challenges in research scale and costs, with the results obtained for a single priority species being used to explore the conservation status and drivers of multiple species. This species richness

approach provides more accurate estimates than traditional asymptotic/non-asymptotic species richness calculations by incorporating detection probability differences between species and can bolster occupancy studies by providing more comprehensive insights at a scale more suited to management strategies. Understanding the relationship between anthropogenic and environmental factors and species richness can improve conservation efforts inside and out of PAs as a whole. This study only included five mesocarnivore species yet demonstrated that these methods can easily be adapted to look at total species habitat use and richness across landscapes.

Effectively conserving all carnivores will require landscape level conservation and calls for increased focus on mesocarnivore populations outside of PAs. Both this study, and previous research, shows that PAs alone are not effective at conserving biodiversity (Glennon and Didier, 2010; Drouilly, Clark and O'Riain, 2018; Kearney *et al.*, 2018). Thus, the uncontrolled culling and eradication of mesocarnivores prevalent in human-dominated landscapes, paired with inadequate conservation of the guild within PAs, may mean that the current IUCN conservation status of "least concern" may have to be revised (Table 2.2). Further work on mesocarnivores in other PAs is important to confirm or support the trends reported in my study and evaluate if these low mesocarnivore numbers are restricted to KZN or a manifestation of PA management strategies as a whole. Mesocarnivores are critical components of healthy ecosystems providing critical ecosystem services. Their absence from select reserves and general scarcity within PAs in the province of KZN is an important finding that argues for further long-term monitoring and research.

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6 | APPENDIX

Table A1 Population density of leopards per 100 km^2 for each PA in 2015, estimated using spatially explicit capture recapture (SCR) analysis by Panthera. PAs include the Eastern Shores Section of iSimangaliso Wetland Park (Eastern Shores), Hluhluwe-Imfolozi Park (HiP), Ithala Game Reserve, Somkhanda Game Reserve, Tembe Elephant Park, uMkhuze Game Reserve and Zululand Rhino Reserve (ZRR).

PA	Mean $\pm$ SD
Eastern Shores	11.81 ± 2.31
HiP	5.05 ± 1.00
Ithala	9.62 ± 1.61
Somkhanda	2.89 ± 0.84
Tembe	5.15 ± 1.32
uMkhuze	5.66 ± 1.38
ZRR	0.69 ± 0.36

Table A2 Relative abundance index (RAI) for three apex carnivores, leopard (*Panthera pardus*), lion (*Panthera leo*) and spotted hyaena (Sp. hyaena; *Crocuta Crocuta*), detected for each PA in 2015, namely Eastern Shores Section of iSimangaliso Wetland Park (Eastern Shores), Hluhluwe-Imfolozi Park (HiP), Ithala Game Reserve, Somkhanda Game Reserve, Tembe Elephant Park, uMkhuze Game Reserve and Zululand Rhino Reserve (ZRR).

	Leopard	Lion	Sp. hyaena	Total
Eastern Shores	186	0	220	406
HiP	118	80	290	488
Ithala	247	0	1	248
Somkhanda	53	0	28	81
Tembe	109	240	1	350
uMkhuze	103	44	127	274
ZRR	72	82	28	182

Table A3 Percentage cover of vegetation types across seven surveys PAs in 2015 (SANBI, 2006). Dominant vegetation types in bold. PAs include the Eastern Shores Section of iSimangaliso Wetland Park (Eastern Shores), Hluhluwe-Imfolozi Park (HiP), Ithala Game Reserve, Somkhanda Game Reserve, Tembe Elephant Park, uMkhuze Game Reserve and Zululand Rhino Reserve (ZRR).

Vegetation Type	Eastern Shores	HiP	Ithala	Somkhanda	Tembe	uMkhuze	ZRR
Freshwater Lakes	1.417				0.014	2.654	
Ithala Quartzite Sourveld			38.269				
Lowveld Riverine Forest		0.062				8.692	
Makatini Clay Thicket						21.643	
Mangrove Forest	0.114						
Maputaland Coastal Belt	19.985						
Maputaland Pallid Sandy Bushveld					13.483	0.393	
Maputaland Wooded Grassland	16.071						
Muzi Palm Veld and Wooded Grassland					6.160		
Northern Coastal Forest	**26.556**						
Northern Zululand Mistbelt Grassland			1.037				
Northern Zululand Sourveld		22.003	9.230	28.721			
Paulpietersburg Moist Grassland			6.981				
Sand Forest	3.496				25.056	0.474	
Scarp Forest		2.213					
Southern Lebombo Bushveld						22.758	
Southern Mistbelt Forest			0.013				
Subtropical Alluvial Vegetation	2.175	0.199	0.042	0.006		0.572	0.177
Subtropical Freshwater Wetlands	24.761	1.184		0.699	2.634	0.342	0.001
Subtropical Salt Pans						0.006	
Subtropical Seashore Vegetation	1.537						
Swamp Forest	2.847						
Swaziland Sour Bushveld			**41.026**				
Tembe Sandy Bushveld					**52.653**	1.953	
Western Maputaland Clay Bushveld				6.949		**36.267**	0.002
Western Maputaland Sandy Bushveld						4.246	
Zululand Lowveld		**74.339**	3.401	**63.625**			**99.820**
Grand Total	98.960	100.000	100.000	100.000	100.000	100.000	100.000